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A MONOGRAPH OF THE

LAND AND FRESHWATER MOLLUSCA

OF THE BRITISH ISLES.

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Fig. 1.

Fig. 2.

Fig. 3.

Fig. 4.

Fig. 5.

Fig. 6.

Fig. 7.

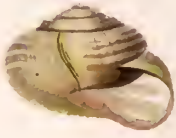

Fig. 8.

Fig. 9.

Fig. 1. *Helix aspersa var. zonata* Moq. Folkestone, collected by Mrs Fitzgerald. Fig. 2. *Helix aspersa var. albo-fasciata*, Jeffreys, Garden, Tuxford, Notts, collected by Mr. W. A. Gain. Fig. 3. *Helix aspersa var. flammea*. Picard, Garden, Tuxford, Notts. collected by Mr. W. A. Gain Fig. 4. *Limnæa peregra var. involuta*, Thompson, Lough Crincaum, Killarney, collected by Mr. W. F. de Vismes Kane Fig. 5. *Limax maximus var. férussaci*, Moq. (after Férussac.) Fig. 6. *Limnæa stagnalis var. appressa*. Say, Lake Michigan, U.S.A. collected by Rev. E. C. Bolles. Fig. 7. *Helix pisana var. magna* Rossm. (after Rossmässler). Fig. 8. *Helix nemoralis var. roseo-labiata*, Taylor. Blagdon, Somerset, collected by Miss F. M Hele. Fig. 9. *Helix hortensis var. lilacina*, Taylor, Chislehurst, Kent, collected by Mr S. C Cockerell.

MONOGRAPH

OF THE

LAND & FRESHWATER MOLLUSCA

OF THE

BRITISH ISLES.

BY

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WITH THE ASSISTANCE OF
W. DENISON ROEBUCK, F.L.S., THE LATE CHARLES ASHFORD,
AND OTHER WELL-KNOWN CONCHOLOGISTS.

STRUCTURAL AND GENERAL VOLUME.

LEEDS:
TAYLOR BROTHERS, PUBLISHERS.

1894–1900.

PREFACE.

The present work was undertaken with the object of placing in the hands of those interested in the conchology of this country a treatise dealing comprehensively and in detail with the many points of interest presented by our native species of land and freshwater mollusca.

Hitherto, with few exceptions, the published works have viewed this subject from very restricted standpoints, and have not attempted to convey any detailed information of the intricate and marvellous organization of the mollusca, nor to give any really comprehensive survey of the subject or discuss the bearings their study could have upon the larger problems that are yet far from solution by the scientific world.

Very many years have been devoted to the study of the subject in its various aspects and to the accumulation of information, in which labours I had for some years the co-operation of my late dear friend, Mr. Charles Ashford, to whom much of the anatomical detail given in the work is due. Mr. W. Denison Roebuck, F.L.S., was also for a lengthened period closely associated with me in its preparation and still practically evinces in many helpful ways his deep interest in its success, and it is in grateful recognition of the generous assistance I have received that I associate their names with my own upon the title-page.

The Council of the Conchological Society have practically demonstrated their lively interest in my work by kindly permitting me to retain in my own possession a considerable part of the society's library, a favour which has been of the greatest assistance to me; while Mr. W. E. Hoyle, M.A., of the Manchester Museum, has laid me under heavy obligation by procuring me the opportunity of examining many scarce books, which otherwise I should have had a difficulty in obtaining. Prof. Paul Pelseneer, of Gand, has also given me valuable aid

and advice upon many critical points, and has at all times placed his great knowledge and experience freely at my disposal, a favour I cannot too cordially acknowledge.

Many other friends have likewise contributed valuable and valued information and assistance, and most of these obligations have been acknowledged in their appropriate places in the text, but the willing co-operation of many other well-wishers has been invaluable, and I may especially mention Mr. R. D. Darbishire and Mr. Robert Welch, to whom I am under so many and such varied obligations for their unwavering interest in, and practical sympathy with, my labours, that thanks are inadequate to express my appreciation of their help.

Although more than six years have been occupied in the production of the present volume, the time cannot be considered excessive when it is remembered that my time cannot be devoted exclusively to the work and that the whole of the labour has devolved solely upon myself, not only as regards the preparation of the text, but also in producing the drawings and photograms from which the whole of the 737 figures or maps have been engraved or lithographed.

Financially, the work is not and cannot be a success, as no expense has been spared to attain the very best results, so that even if the whole of the small edition that has been prepared becomes exhausted, the proceeds will not be nearly sufficient to repay even the pecuniary outlay involved in its production.

The portion of the work devoted to genera and species will be commenced without unnecessary delay and, it is hoped, will be quickly completed, but to attain this desirable result I must bespeak the active aid of all those interested in the subject.

JOHN W. TAYLOR.

North Grange, Horsforth,
Leeds, *Dec. 29th, 1900.*

CONCHOLOGY:

STRUCTURAL AND GENERAL.

A

MONOGRAPH

OF THE

LAND AND FRESHWATER MOLLUSCA

OF THE

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Definition of Conchology.

Conchology, the term by which the study of the mollusca is most generally known, is a combination of the Greek words, κόγχη (a shell-fish), and λόγος (a discourse or treatise); and is usually understood to embrace the study of the complete subject—not merely the shell, but also the animal which forms it. By some authors the term has been restricted to the study of the shell only, and the word *Malacology* used to designate the investigation of the animal or soft parts; although Tryon and some other scientists have proposed that Malacology shall be understood to embrace the complete subject, and supersede the older name.

The molluscan sub-kingdom embraces those organisms with soft and fleshy bodies, enclosed or covered by a muscular sac which is called the mantle, and which usually secretes a more or less regular and symmetrical shell, mainly composed of carbonate of lime, the chief function of which would appear to be the protection of the vital organs of the body. In some genera the shell is internal or concealed beneath the mantle, it is then usually of a simple flattened plate-like form or even reduced to a few granules.

The Mollusca are distinguished from the Articulata, by their bodies not being segmented, and also by their nervous system consisting of

several pairs of irregularly disposed ganglia, which arrangement led Professor Owen to apply the term Heterogangliata to them, in contradistinction to Homogangliata, by which term he designated the Articulata on account of their ganglia being arranged in a paired longitudinal series. From the Vertebrata, they are distinguished by the absence of an internal bony skeleton.

History.

The extensive and important sub-kingdom Mollusca (*mollis*, soft), as now understood, embraces four Classes only, Cephalopoda, Gastropoda, Scaphiopoda, and Pelecypoda.

The *Polyzoa*, *Brachiopoda*, and other groups, which were formerly included, have been successively removed from the molluscan sub-kingdom and placed in other divisions.

Linné originally separated the sub-kingdom Mollusca as now understood, into two great divisions, placing the shell-bearing species associated with other organisms in a group he designated as *Vermes Testacea*, and the naked, or internally-shelled species, he grouped with many other very different forms of life, and designated them *Vermes Zoophyta*, a term which he afterwards changed to *Vermes Mollusca*.

Baron Cuvier was the first to unite the Mollusca into one great sub-kingdom, and though he excluded many groups of organisms which were united with them by Linné, he still retained several which have been since excluded by more modern authors.

Our British land and freshwater mollusca belong exclusively to the two classes, Gastropoda and Pelecypoda, the remaining groups being exclusively marine in habit.

Classification.

Classification has for its object, not only the systematic arrangement of the objects of study, but the combination in suitable groups of those species having most affinity with each other, and possessing in common some recognizable determinate characters. When a number of species possess this suitable similarity of organization they are united in a group termed a GENUS; such of these groups or genera as are distinguished by some common character are united in larger groups, called FAMILIES; these larger groups or families are gathered into still more numerous assemblages, termed ORDERS; and finally

combined into CLASSES. All these divisions should possess in common, some peculiarity of greater or lesser importance, and all these groups are or may be sub-divided into sections, which with the prefix of SUB-, indicate the possession of characters of lesser importance than those distinguishing the chief groups.

The Animal Kingdom is divided into several Sub-kingdoms, the Vertebrata standing at the head, and by general concurrence among scientists, the Mollusca occupy the second place, preceding the Articulata and every other sub-kingdom.

The Mollusca may be primarily divided into four Classes, based upon the modifications of the foot or locomotive organ, and named CEPHALOPODA, GASTROPODA, SCAPHOPODA, and PELECYPODA. The Pteropoda, which formerly constituted a fifth class, are now considered to be Opisthobranchiate Gastropods. Two of these classes are exclusively marine, leaving only the Gastropoda and Pelecypoda, to which groups our British land and freshwater shells exclusively belong. The names Gastropoda and Pelecypoda, refer to the morphological peculiarities of the animals, the alternative terms Univalve and Bivalve, which are also in general use, respectively expressing the character of the shells.

The GASTROPODA are characterized by the development on the ventral side of the body of a sole-like locomotive disc or foot, and by

FIG. 1.—An Anisopleurous Pulmonate Gastropod.
Helix aspersa v. *zonata* Moq.,
Folkestone, collected by Mrs. Fitzgerald.

its undulatory or wave-like expansions and contractions the creature moves. This class may be primarily divided into two groups or Sub-classes, ISOPLEURA and ANISOPLEURA, according as the chief viscera have or have not been subjected to a torsion and a semi-rotation, bringing the termination of the alimentary canal from its presumed ancestrally posterior and medial position, towards an anterior or lateral one, involving in this movement other organs and their ducts; this change of position is assumed to have been caused

by and owing to the development of the shell as a protection and covering to the vital organs of the body, and this shelly covering not having retained its equilibrium has fallen over to one side and

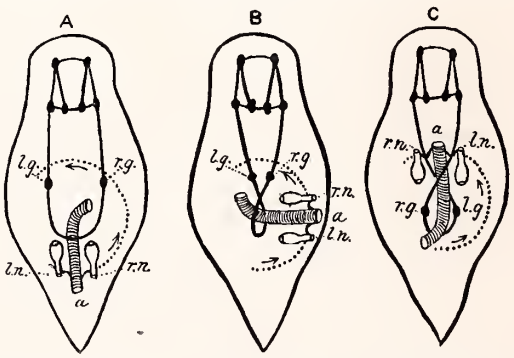


Fig. 2.—Diagrams illustrating the progress and method of the assumed rotation of the internal organs in the Anisopleura (after Lankester). The arrows indicate the direction of the rotatory movement. A. unrotated ancestral condition; B. semi-rotation of the organs partly accomplished; C. complete semi-rotation.— *a.* anus; *l.n.*, *r.n.* the primarily left and primarily right nephridia or kidneys; *l.g.* primarily left visceral ganglion, which after the torsion is accomplished forms the sub-intestinal ganglion; *r.g.* primarily right visceral ganglion, which subsequently becomes the supra intestinal ganglion.

to the rear, compressing and gradually displacing the termination of the intestine and causing it to assume the position it now occupies. The Isoplenra, of which the *Chitons* are examples, are practically organized in a bilaterally symmetrical manner externally and internally, the viscera not having been subjected to the torsion alluded to. The Anisopleura to which all our land and freshwater species belong, though presenting externally a bilaterally symmetrical appearance of the head and foot, have been subjected to changes in the position of the chief viscera by this semi-rotation of the visceral sac; they may be sub-divided into two Orders called Euthyneura and Streptoneura, this separation being based upon the modification caused in the arrangement of the visceral nerve-loop, by its being involved in, or escaping from, the twisting of the viscera. In the Enthyneura, of which *Limnæa stagnalis* is an example, the visceral nerve-loop is often comparatively short, and on account of lying beneath the intestinal canal has escaped the twisting to which the upper portion of the viscera has been subjected. The Streptoneura differ from the Euthyneures owing to the visceral nerve-loop lying above the intestines and being thus involved in the twisting and rotation the organs have undergone,

and consequently made to assume the form of the fig. 8 as in the *Viviparidæ*.

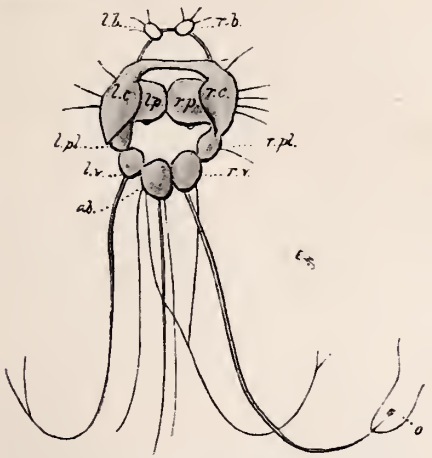


FIG. 3.—Nervous system of *Limnæa stagnalis*, as typical of the short looped Euthyneurous condition (modified after Lankester). *r.b.* and *l.b.* right and left buccal ganglia; *r.c.* and *l.c.* right and left cerebral ganglia; *r.p.* and *l.p.* right and left pedal ganglia, with the otocysts on their inferior face; *r.pl.* and *l.pl.* right and left pleural ganglia; *r.v.* and *l.v.* right and left visceral ganglia, the long nerve to the osphradium or olfactory organ *o*, is given off from the right visceral ganglion; *ab.* unpaired abdominal ganglion.

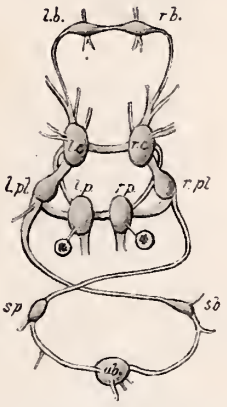


FIG. 4.—Nervous system of *Vivipara* as a type of the Streptoneurous condition (after Ihering). *r.b.* and *l.b.* right and left buccal ganglia; *r.c.* and *l.c.* right and left cerebral ganglia; *r.p.* and *l.p.* right and left pedal ganglia with the otocysts on short pedicels; *r.pl.* and *l.pl.* right and left pleural ganglia; *s.b.* and *s.p.* the sub and supra-intestinal ganglia; *ab.* unpaired abdominal ganglion.

In our British species of land and freshwater shells, the orders Streptoneura and Euthyneura are exactly equivalent to the groups Operculata and Inoperculata respectively, with perhaps the doubtful exception of *Neritina*. The Streptoneures are divided into two Sub-orders, ZYGOBRANCHIA and AZYGOBRANCHIA, the first-named embracing those Streptoneurous species in which although the semi-rotation of the organs has taken place and the gills and other organs become transposed in position, have yet retained their bilateral symmetry, the common Ormer or Ear-shell, *Haliotis tuberculata* is an illustration.

FIG. 5.—A Streptoneurous Azygobranchiate Gastropod. *Valvata piscinalis* Müll. × 3, Sway, Hants., coll. by Mr. C. Ashford. *ct.* ctenidium or exsertile branchial plume; *r.ct.* filiform appendage, probably the vestigial rudiment of the primitively left branchial plume.

The Azygobranchiata, of which *Vivipara* and other Prosobranchs are more or less typical, differ from the preceding group, owing to the compression and twisting of the viscera having led to the loss of one of

the component parts of several of the paired organs, thus the original left gill and other organs have become atrophied, but the right gill, etc., retained, though owing to the rotatory movement the viscera have been subjected to, these originally dextrally placed organs are now placed to the left of the rectum. The Azygobranchia may be separated into two sections: PULMONATA and PECTINIBRANCHIATA, containing the animals breathing air and water respectively, the former composed of those species which have become modified and adapted to a terrestrial life and aërial respiration termed Pneumonochlamyda by Lankester, and Neurobranchiata by Macalister, of which *Cyclostoma elegans* is an example; while the Pectinibranchiata embrace all the operculate aquatic species.

FIG. 6.—Gill or Ctenidium of *Vivipara*, a Pectinibranchiate Gastropod (after Lankester). *i.* intestine running parallel to axis of gill and ending in the anus *a.*; *br.* rows of elongate branchial filaments.

FIG. 7.—Diagram of the Lung of a Pulmonate Gastropod, *Helix aspersa* L. *n*, nephridium, with ureter crossing its surface; *r.* rectum; *a.* auricle; *v.* ventricle; *b.b.* canal bringing blood from hinder part of body; *c.c.* canal communicating with body cavity and also bringing blood to lung. The darker veins carry the blood from these canals to surface of lung; the light veins recollect and convey to auricle after aëration.

The Euthyneurons Gastropods comprise two Sub-orders, based upon the position and function of the respiratory organs, viz.: PULMONATA and OPISTHOBRANCHIATA: of the latter group the marine genus *Bulla* is an example, and the Euthyneurons Pulmonates comprise the bulk of our native land and freshwater mollusks. Though I have classed together the Euthyneurous air-breathers as simply Pulmonata, it should be mentioned that some Biologists do not regard the pulmonary sac of the *Helicidæ* as homologous with that of the *Limnæidæ*: the respiratory cavity in the former being said to be a modification of the cloaca of the kidney, hence the term NEPHROPNEUSTA applied to them; while that of the

Limnæidæ is considered to be identical with the branchial chamber of the Pectinibranchs, the term BRANCHIOPNEUSTA being used to express this difference. Finally the Pulmonates are separated into two Sections based upon the position of the eyes: the STYLOMMATOPHORA, which are all terrestrial species and have the eyes placed at or near the tips of the upper tentacles as in *Helix*, *Succinea*, etc.; and the BASOMMATOPHORA, which includes those species or genera in which the eyes are placed at or near the base of the tentacles, as in *Limnæa*.

FIG. 8.—A Stylommatophorous Pulmonate. *Succinea putris* (L.), Ashley Marsh nr. Bristol, Collected by Miss Hele.

FIG. 9.—A Basommatophorous Pulmonate. *Limnæa peregra* var. *ovata* Drap., R. Torne, Doncaster.

The class PELECYPODA (πελεκυς an axe and ποδ–a foot, or axe-footed), are exclusively aquatic and pre-eminently marine species,

FIG. 10.—An Equivalve Inequilateral Pelecypod. *Unio pictorum* (L.), showing left valve, Clumber Lake, Notts., collected by Mr. C. T. Musson, F.L.S. *a.s.* anal or excurrent siphon; *br.s.* branchial or incurrent siphon; *f.* foot.

characterized by the possession of a somewhat linguiform extensile foot, usually more or less adapted for ploughing through or burrowing in sand and mud, and are further distinguished by the development of an external shell composed of two pieces, or valves, joined together by an elastic ligament at the dorsal or upper margin, and often furnished in addition with interlocking teeth or denticles at the hinge. The term Bivalve, by which they are widely and popularly known, has reference to this universal presence of two valves to the shell, while LAMELLIBRANCHIATA which is also very generally used refers to the lamellar or leaf-like character of their branchiæ or

gills. The class may be first divided into three Orders, according to the number and development of the Adductor muscles. This mode of classification, though perhaps not perfectly satisfactory, seems preferable to the various other methods of division that have

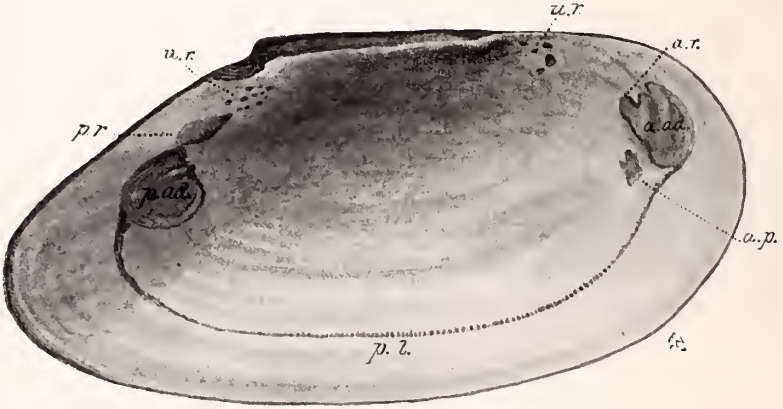


Fig. 11.—An Isomyate, Integripalliate Pelecypod.
Anodonta cygnæa (L.), left valve,
Clumber Lake, Notts., collected by Mr. C. T. Musson, F.L.S.
a.ad. anterior adductor scar; *p.ad.* posterior adductor scar; *a.r.* anterior pedal retractor scar; *p.r.* posterior pedal retractor scar; *u.r.* umbonal or lesser retractor or retentor scars; *a.p.* anterior pedal protractor scar, the abdominal retentor scar of Clessin; *p.l.* pallial line.

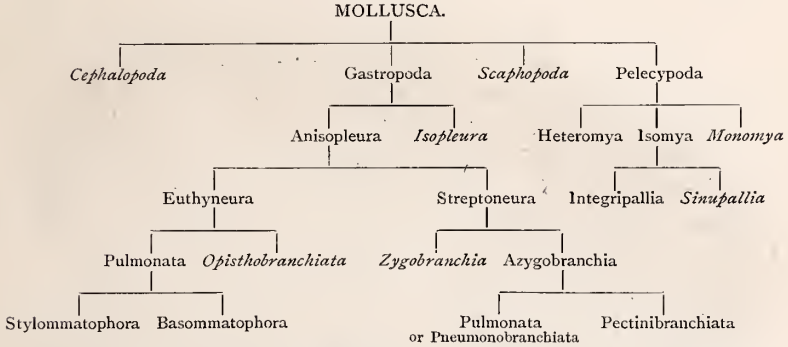
at different times been proposed: the Monomya, or one-muscled as the Oyster; Isomya, in which those muscles are two in number, and approximately equal in size, as exemplified in the *Unionidæ*; and Heteromya, in which, although two muscles are still developed, the anterior one is much smaller than the posterior one, as in *Dreissensia*. Sub-orders are formed in the Isomya, by the presence or absence of a conspicuous sinus or indentation in the pallial line, indicating when present the possession of extremely long retractile siphons, and thence called Sinupallia, as expressing the indication the pallial line affords. The Integripallia, to which all our species belong, have a non-sinuated pallial attachment.

Fig. 12.—A Heteromyate Pelecypod.
D. polymorpha (Pallas), Gloucester Canal, Stroud, Coll. by Mr. E. J. Elliott.
a.ad. ant. adductor scar; *p.ad.* post. adductor scar; *p.r.* post. pedal and byssal retractor scar; *p.l.* pallial line; *l.* ligamental pit.

The classification adopted is given also in tabular form, so that the inter-relationship of the different groups can be understood at a glance.

TABULAR VIEW OF THE SUB-DIVISIONS OF THE MOLLUSCA, ARRANGED TO SHEW THEIR ASSUMED GENETIC RELATIONSHIP.

The groups printed in italics are those not represented amongst the British Land and Freshwater Mollusca.



In all attempts at classification, it is necessary to carefully discriminate between species showing similarity of form and habit but not structurally conformable, and those in which the whole organism is in harmony with the external aspect and mode of life. The first show analogical relation only, but the latter are related homologically and should therefore be classified together. If the resemblances exist from a very early age, they are considered to be of the greatest importance and to imply community of descent.

Almost every organ of the body has been proposed, at one time or another, as a basis for the better arrangement of the Gastropoda, the circulatory, nervous, reproductive, alimentary, and respiratory organs, as well as the presence or absence of the operculum, the arrangement and position of the eyes, etc., have all been or are now used separately or together for the purposes of classification.

In the Pelecypoda, the muscular and respiratory systems have been strongly relied upon for chief divisions; the characters of the hinge, with its interlocking teeth, and the development or absence of the siphonal tubes, have also, always been considered to be important features, but too much reliance should not be placed on any one character for taxonomic purposes, and confirmation should always be sought by other organs, as it will be readily conceded by everyone that all organic characters are of varying importance according to circumstances, and this must of necessity be so in a natural classification based upon the general organization and affinities of the animal and

its shell, and not founded upon any particular organ, or set of organs, arbitrarily selected as in an artificial arrangement.

In former times, before the structure of the Mollusca was systematically examined, or its significance understood, they were arranged according to the different shapes of the shells. Linné was one of the first to lay stress upon the structural details of the shell, noting the character of the umbonal teeth, ligament, folds, sculpture, etc., and using them to separate various groups. He also attached great importance to the form of the animal, and ranged all mollusks under five heads, as *Doris*, *Limax*, *Tethys*, *Sepia*, and *Ascidia*, which division coincides in some measure with the classes accepted at the present day.

Adanson introduced the system of classifying the bivalves in accordance with the muscular impressions, and took note of the operculum in Gastropods as an important character.

The use of Physiological characters was first suggested by Cuvier, who established an arrangement based upon the peculiarities of the respiratory organs, and brought together all the pulmonate species; he also proposed the still accepted terms, designating some of the higher groups.

Lovén and others have proposed the use of the lingual armature, as suitable organs for establishing an improved arrangement of the Gastropoda, and the figures that have been published have often confirmed the truth and value of the older genera, established solely upon the morphology and character of the shell.

H. von Ihering advocates the use of the nervous system in preference to the radula, respiratory organs, or other single character; and I have followed Prof. Ray Lankester and adopted this system for dividing two very important groups in the Gastropoda.

All classification, however, upon whatever basis it exists, which places the objects in rotation, must be to a certain extent arbitrary and artificial, and of necessity violate the affinities of some of the groups or species, because it may well be that those selected to precede or follow any particular species or group may be no closer allied in general organization, than one or more others necessarily removed further away. If this be so, then no hard and fast line can truthfully be drawn as to the proper sequence of many of the different groups or species, and we can only place the species or groups, as the case

may be, in such order as appears to us to do the least violence to their natural relationships, and cannot reasonably stigmatize as incorrect or unscientific, as is so often done, a different arrangement, in which other characters are allowed to have more weight than we personally are disposed to give them.

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Nomenclature.

The universal acceptance of the binomial system of nomenclature, by the scientists of all countries, by which practice two names, a generic and a specific one are applied to every distinct species—exactly equivalent to the use among mankind of the christian name and surname—the generic name indicating the group to which the species

belongs or is most closely related to, while the specific name decisively separates it from all others in the genus, one name thus showing the affinity of the organism and the other its divergence Formerly the use of a series of descriptive epithets was in vogue to indicate species and must have proved in practice very cumbrous and unwieldly, as the synonyms I shall presently give under the specific heads will sufficiently show.

Linné, though not the originator of the binomial system, was the first to apply it to the whole of the animal and vegetable kingdoms, and it has therefore been decided that recognized nomenclature shall be considered to take its origin from him and date from 1758, the year of publication of the 10th edition of the "Systema Naturæ," in which work he first applied the binary system of nomenclature to all organisms, which he had only partially done in the previous editions. All names or epithets given to species prior to 1758 are therefore not recognized in the nomenclature, except as synonyms, but the earliest name published after that date if accompanied by a recognizable description or figure is adopted and should not be altered, except when mis-spelt by author or printer. The name of the person who proposed the name, should in all cases follow that of the species he has discriminated, but if the species is afterwards removed from the genus in which it was placed by him, this is indicated by placing the author's name in parentheses, thus *Arion ater* (L.) was originally described by Linné as *Limax ater*, and the use of the parentheses indicates the generic change; while *Helix nemoralis* Linné retains its original generic position, as is shown by their absence.

Some naturalists still consider that the author establishing the genus should append his name to all the species embraced in it, and this opinion has led to the alteration and division of many of the genera. Scientists generally do not however agree with or accept this doctrine, and little can be said in its favour.

The classical languages—Greek and Latin—are, by general consent, chiefly used for the names of natural history objects; the names of Families and Sub-families being formed by the addition of idæ and inæ respectively, to the genitive form of the name of the principal or typical genus, this addition being made after the elision of the last syllable, thus *Helicidæ* and *Helicinæ* respectively indicate the Family and Sub-family of which the genus *Helix* is typical.

GENERIC names, which are essentially substantives, are taken preferably from the Greek language, though they may also be taken from the Latin or other tongue, but if the word be not Latin, it should be treated as such and Latinized in the regular and orthodox way, and should in writing or printing always commence with a capital letter. A generic name should consist of a single word, which may be either simple or compound. In the compound or composite words the attribute should always precede the chief term, as in *Cyclostoma*. If the generic term is used in the adjective form, which is not desirable, it should always take the feminine termination.

GENERIC names may be

Greek substantives, for which the rules of Latin transcription must be followed, as in *Ancylus*, *Physa*, etc. These rules require that αι be rendered as *æ*; ει as *i*; ου as *u*; οι as *œ*; υ as *y*; θ as *th*; φ as *ph*; χ as *ch*; κ as *c*; γχ as *nch*; γγ as *ng*; ' as *h*; ος and ον if terminal are rendered as *us* and *um* respectively.

Compound Greek words, the attribute being always placed first, as in *Stenogyra*, *Cyclostoma*, etc.

Latin substantives, as *Auricula*, etc.

Compound Latin words, as *Semifusus*, etc.

Derivatives from Greek or Latin words, expressing diminution, comparison, resemblance, etc., as *Helicella*, *Helicina*, etc.

Mythological and Ancient words or names, as *Venus*, *Cleopatra*, etc., the words or names taking the Latin termination if not already possessing it.

Modern names; these preserve their orthography and retain any accents with which they may be surcharged, and if terminated by a consonant add ius, ia, ium to the full and complete name of the person to whom the dedication is made, as *Dreissensia*, *Mülleria*, etc. Names ending in e, i, o, y take the termination us, a, um, as *Wyvillea*, etc., but if terminated by a or u add ia, but, in the latter case, the letter t is interpolated for the sake of euphony, as *Payraudeautia*, etc.

Names of Vessels; according to their character these are treated as mythological names, as *Vega;* or as modern names, as *Challengeria*, etc.

Compound generic terms may be formed by a combination of the names of two other genera, and when this practice serves to express the position and affinities of the group it may be adopted with advantage, as in *Ariolimax*, etc.

Names formed anagrammatically, as *Milax*.

The employment of generic names already in use in other departments of Zoology is not desirable, and wherever possible should be avoided.

The Specific names should be formed of a single word, preferably a Latin adjective or substantive, of a short and euphonious character, though Latinized Greek words and undeclinable words of other languages may be admitted, and should be written or printed with a small initial; though upon this point there is some difference of opinion amongst authors, some using an initial capital letter for personal and geographical names and a small initial for all others. In certain cases where the name of the object after which the organism is named is formed of two words, the specific name may be double also, as *H. sancte-helenæ*; or where a comparison is sought with another object, as in *A. cornu-arietis*, the two words may be legitimately used, but should always be connected by a hyphen.

Specific names may be

Substantives or adjectives recalling some character or peculiarity of the species, as *fontinalis, auricularia*, etc.

Names of persons to whom the species may be dedicated; these if in the genitive case are formed in masculine names by the addition of a simple i to the full and exact name of the person to whom the species is dedicated, as *sowerbyi*, or the name may be used in the adjective form taking the termination anus, ana, or anum, in accordance with the generic term, as *sowerbyanus*. In feminine names the diphthong æ is added to or combined with the name to be Latinized as *turtonæ, emmæ*, etc. In those cases where the name has been employed and declined in the Latin tongue, it will follow the regular declension, as *sempronii*.

Geographical names if known to the Romans or Latinized by the mediæval writers, should also be in the genitive or in the adjective form, as *antillarum, burdigalensis, ægyptiacus*, etc. If the names have not been used in Latin

the exact orthography of the radical is preserved, with any accents with which it may be surcharged, the word being used in the adjective form and receiving the suffix ensis, ius, icus, inus, itus, etc., if the genus be masculine, as in *alzenensis*, *helveticus*, etc., the last syllable varying in accordance with the gender of the generic term.

If the radicals of geographical or other names give rise to two or more too closely similar derivatives, as *hispanus* and *hispanicus* ; or *fluvialis*, and *fluviatilis*, these should not be employed concurrently to distinguish different species in the same genus.

Greek prefixes or suffixes should only be combined with words derived from the same language : but those of Latin origin are more generally used, as scientific terms are essentially Latin in character.

The repetition of the same word for the generic, the specific, or the varietal name of a species is undesirable and should whenever possible be avoided.

Trinomialism is an extension of the Linnean method of nomenclature, by the addition of a third name, to indicate the more important phases of specific variation, which name is preferably derived from the Latin language, and in construction and modification is subject to the same rules as the specific names : if, however, the word Varietas in either its full or contracted form be interposed between the specific and varietal name, the varietal term if in the adjective form, should always take the feminine termination : Example, *Sphærium lacustre* var. *brochoniana* Bourgt. If, however, that word is not interposed, and it is not essential that it should be, then the varietal name must accord in gender with the generic term : Example, *Sphærium lacustre brochonianum* Bourgt.

Monstrosities when named, which is seldom desirable, take the neuter termination, if the word Monstrum, or one of its contractions, is interposed between the specific and monstral names, the latter being in the adjective form: Example, *Limnæa peregra* m. *sinistrorsum* Jeffr., but when the word Monstrum is omitted, the trinomial term must agree with the generic name, as in the varieties : Example, *Limnæa peregra sinistrorsa* Jeffr.

Though it is desirable that a name should recall or indicate some character or peculiarity of the organism, it is not absolutely essential that it should do so, as a name is simply a name, mark, or

symbol set upon objects to distinguish them from others, and is not a definition of their characters. Many scientists, however, owing to the difficulty of finding appropriate and characteristic names which express some quality peculiar to the species, not shared in a greater or lesser degree by others in the same genus, decidedly prefer and advocate names which are only arbitrarily connected with the organism and denote or imply no character or peculiarity of the object. It is, however, very desirable that an uniform and conventional code of names should be used to indicate the same mode of variation in the different species; thus *alba* could be used to designate the pure white or albine shells, the term *albida* being reserved for the whitish forms, when it is considered necessary to give them a special designation; *rufa* could be employed for the rufous specimens, *hepatica* for the liver-coloured ones, *rosea* for the pink ones, etc., etc. Variations of form, sculpture, size, thickness, markings, etc., could be similarly indicated by appropriate, expressive, and euphonious terms, the great aim being to ensure as far as practicable the application of the same term to the same character of variation, in every species.

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Synonymy.

From the wide distribution of many species, the great number of scientific publications in many languages, and the earnest pursuit of scientific study by a constantly increasing number of students, it almost necessarily follows that many species have names bestowed upon them by more than one person, either from ignorance of each

other's labours, from a personal conviction of the unsuitability of the name previously applied, or, from a misapprehension of specific characters, which leads them to confuse one species with another, and therefore apply their names incorrectly: thus Draparnaud mistook the French form of *Helix cantiana* for *Helix cartusiana* and thereupon, in the belief that the shell was new to science, described the true *cartusiana* as *Helix carthusianella* ; the synonymy of the two species in reference to this illustrative incident is shown as follows :—

Helix cantiana Mont.	*Helix cartusiana* Müll.
Helix carthusiana Drap. *non* Müll.	*Helix carthusianella* Drap.

The variability and wide dispersal of *Limnæa peregra*, and consequently the protean forms assumed under different conditions of existence by this variable and mobile species, have led to its various modifications being designated by very numerous names intended to denote in the opinion of their authors either specific or varietal differences. For this species alone over three hundred names have been catalogued, all specifically synonymous, and the great bulk of the names applied varietally must also be of the same character and refer to modifications previously discriminated and named.

Probably these evils will never be entirely overcome, and it will therefore be a continual task to investigate and place in the synonymy of the appropriate species the duplicate or incorrect names bestowed or wrongly used from time to time. These incorrectly applied and duplicate names are termed Synonyms.

Some of these names, though applied to species already discriminated and named, may represent strongly marked geographical or zoological variations, and as indicating such are worthy of retention in the varietal nomenclature.

Shell.

The great majority of mollusks have an external covering or shell, which is acknowledged to be so characteristic a feature in the group, that the term Testacea (from *testa* a shell), has been very appropriately applied to them. One distinguished scientist, Prof. Ray Lankester, has even proposed the application of the term Conchifera, or shell-bearing, to the whole of the Mollusca, a name previously restricted to the Lamellibranchs. Although the internal organs of the animal often exhibit more important and permanent characters, yet the close and intimate connection existing between the animal

and its shell, which is also, as truly, an organ of the animal, confirms and supports the importance attached to the shell in classification.

Shells are termed EXTERNAL, when they are capable of containing all or part of the animal; and INTERNAL, when enclosed or concealed within the mantle, and serve not only as a support, but also as a protection to the internal and vital organs, and may be considered to represent

FIG. 13.—An External Shell.
Helix nemoralis L.,
Bitton, near Bath.
Collected by Miss F. M. Hele.

FIG. 14.—An Internal Shell.
Limax maximus L. × 2,
Christchurch, Hants.,
Collected by Mr. C. Ashford.

the internal skeleton of the Vertebrates, giving similar evidence of their natural affinities and relationship, the contour and structure of the shell being always in harmony with the organization of the animal and with their differences in form and composition, establish how exceedingly important is the study of the shell itself, and to geologists especially this importance is vastly increased, as their fossilized remains are the only relics of the vast numbers of now totally extinct species, and from these remains alone, we are able by induction and comparison with our recent forms, to infer with great probability the organization, habits, and habitats of these long extinct organisms and gain some clue to the physical conditions of these remote times.

Though differing considerably in appearance, structure and texture, shells principally consist of an organic chitinous substance and carbonate of lime, with a chemical formula of $CaCO_3$. M. Delacroix has stated that the shell of *Helix pomatia* is composed of 64·96 per cent. of carbonate of lime, 16·40 per cent. of other mineral substances, and 18·64 per cent. of organic matter, but a specimen of the same species from Cheltenham, examined by Mr. Crowther, yielded strikingly different results: the total weight of the shell was 6·298 grams, which analysis showed to be composed of 6·1205 grams of inorganic substances and ·1775 gram of organic matter, or 2·818 per cent. of organic substances and 97·1816 per cent. of carbonate of lime and other earthy salts. An example of *Limnæa stagnalis*, weighing ·681 gram, also examined by Mr. Crowther, yielded on analysis ·6603 gram of mineral matter, chiefly carbonate of lime

and ·0207 gram of organic matter, or 96·96 per cent. of inorganic substances and 3·04 per cent. of organic matter.

The calcareous portion of the shell has always an organic basis, which is first secreted and then gradually impregnated with the carbonate of lime, which latter substance is sometimes deposited in layers of very distinct character. The organic basis, which is termed Conchyolin, maintains the life of the shell, for on the death of the animal it soon disappears and the shell gradually becomes almost pure carbonate of lime, and very brittle; there are, however, in some species traces of carbonate of magnesia, silicic acid, phosphate of lime and minute quantities of other substances. The specific gravity of shells generally is somewhat higher than that of Carrara marble, and many are perceptibly harder than, and will scratch, calc-spar.

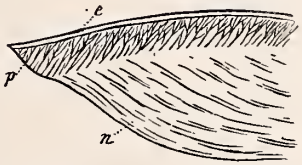


FIG. 15.—Oblique section through the shell of *Unio* (magnified), showing the three layers of which the shell is composed (after Semper).
e. periostracum or epidermis, the external layer; *p*. prismatic or middle layer; *n*. nacreous or inner layer.

The inner layer of the shell, when duller than in nacreous shells, is termed porcellanous, but it is often iridescent or pearly, this charming appearance being caused by the peculiar disposition of the shelly matter in thin overlapping layers with minutely corrugated edges, which diffract the light and thus cause the iridescent effect, the thinner and more transparent the overlapping plates, the more beautiful the lustre. This inner layer is secreted by the whole surface of the mantle and, according to Mr. Carrington, owes its exquisite smoothness in *Helix pomatia* to a surface deposit of almost pure silica. The free glandular margin secretes or forms the middle or prismatic layer, consisting of prisms of carbonate of lime arranged in a particular way.

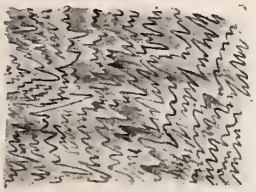


FIG. 16.—Surface of Nacre or Pearl, highly magnified, showing the minute undulations upon which the pearly lustre depends (after Tryon).

The outer surface, epiconch, or periostracum, perhaps better known as the epidermis, is also a product of the collar of the mantle; it is of a chitinous nature with a complex chemical composition said to be represented by the chemical formula $C_{15}H_{26}N_2O_{10}$, and varies remarkably in its thickness and general character, appearing to be analogous to the periosteum of the bones of the Vertebrates. It is

very persistent and almost indestructible and has been observed still adherent to tertiary fossils; its chief office would appear to be to protect the calcareous portion of the shell from the disintegrating influence of external conditions, but on the death of the animal, if the shell is left exposed to the weather, this epidermis is very quickly deciduous, though practically persistent during the life of the animal.

This protective covering is strongly developed and remarkably varied in freshwater shells, and in land species habitually frequenting moist and shaded situations, it is also sometimes the seat of the colouring matter with which shells are often ornamented, but usually the pigment is resident in the calcareous portion of the shell, the epidermis or periostracum being generally of a transparent or semi-transparent horny tint, through which the colouring is seen more or less vividly. In some of the Philippine *Bulimi* the epiconch or epidermis is double, that is formed of two distinct layers, and this peculiarity has been shown by Mr. Tye to be shared by at least one British species, the *Helix arbustorum*; this duplication of the periostracum is best seen in the variety *flavescens*, as the less persistent external film is in that form darker in colour than the inner layer, it however very quickly exfoliates, and is therefore frequently found only in more or less isolated and irregular patches, chiefly upon the body whorl.

The varied sculpture and projecting processes which ornament many species, and are sometimes especially indicative of maturity, or of periodic cessation of growth, have often their internal support and receive their character and form from the calcareous portion of the shell, but the hairy or bristly appendages which distinguish many species would appear to be solely epidermic in origin and character.

Gümbel has demonstrated by experiment the enduring character of the outer or epidermic layer, and shown that carbonic acid gas dissolved the compact portions of shells more quickly than those less closely aggregated, agreeing thus with the observations of geologists, which tend to show that the outer layer of shells is better preserved than the nacreous, and this than the fibrillar layer.

If the carbonate of lime in a shell be removed by acid, the organic residuum may still retain the shape of the shell, forming a sort of membranous framework, as the chitinous epiconch is scarcely affected by ordinary acids, though dissolved by caustic alkali. Mr. Crowther

has demonstrated that a 10 per cent., or even a weaker, solution of hydrochloric acid gives the most perfect and satisfactory results, a stronger solution tending to injure or impair the exquisite delicacy and beauty of this organic covering of the shell substance.

Shells are formed or secreted by the mantle, and are of infinitely varied shapes, consistence and ornamentation, and though organically connected with the animal, are not vascular structures and have therefore no inherent power to repair any injuries they may sustain, but if the injuries are situated at or near the margin of the aperture they are fully and completely repaired by the collar of the mantle, with the pattern and ornamentation perfectly reproduced, as in the normal shell, so that the reproduced portion is often only distinguished with difficulty; if, however, the injuries are remote from the margin, the repairs are entirely made by the visceral mantle and are thus deficient of colour, ornamentation, or epidermis.

FIG. 17.—An Univalve Shell showing injuries remote from the aperture, as repaired by the visceral mantle.
Helix nemoralis L.,
Peel, Isle of Man,
Collected by Mr. E. Collier.

The class GASTROPODA, which includes all our Univalve shells, is the most typical and numerous group of the Mollusca, exhibiting in the highest degree the characteristics of the sub-kingdom, and showing least affinity in structure with other organisms.

The shell, with few exceptions, is composed of one single piece or valve, hence the term Univalve, though Woodward considers this single piece to be homologous with the two shells of a Bivalve united above. The shell is usually of a conically tubular form, enrolled more or less closely around a central axis, thus diminishing the space occupied and securing a more portable and compact shell, and is, with a few exceptions, coiled dextrally—that is, from left to right. It is in most species quite easy to distinguish a dextral from a sinistral shell. A simple method is to hold the shell with its apex upwards and its mouth directed towards you, when if the

FIG. 18.—A Dextral Univalve.
Helix nemoralis L.,
Piperstown, Co. Louth,
Collected by Miss S. Smith.

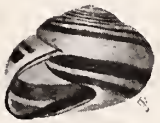


FIG. 19.—A Sinistral Univalve.
Helix nemoralis m. *sinistrorsum* Fér.
Sandhills, Bundoran, Co. Donegal,
From Miss F. M. Hele.

aperture is on your right hand the shell is dextral, if on your left, sinistral, as shown in the foregoing figures.

The length of the tube, its shape, and its closer or more open mode of convolution, gives rise to a great variety of forms amongst the different species, the principal of which are :—

ELONGATE, TERETE, or SUBULATE, when the shell has the spire greatly produced and pointed, as in *Helix acuta* Müll., *Cæcilioides acicula* (Müll.), *Balea perversa* (L.), etc.

FIG. 20.—Example : *Helix acuta* Müller, Point Scarlet, near Castletown, Isle of Man, collected by Mr. A. Taylor.

TURRETED, when the shell is elongate, but the upper portion of the whorls are shouldered or angulated, as in *Limnæa truncatula* (Müll.).

FIG. 21.—Example : *Limnæa truncatula* var. *turrita* Clessin, ditch, Bierley, near Bradford, Yorks.

CYLINDRICAL, when the shell is cylindrically elongated, as in *Pupa muscorum* (L.), *Vertigo edentula* (Drap.), etc.

FIG. 22.—Example : *Pupa muscorum* var. *elongata* Clessin × 3, rejectamenta of River Stour, Sandwich, Kent, collected by Mr. S. C. Cockerell.

FUSIFORM, or SPINDLE-SHAPED, when the shell is swollen in the middle and tapering at each end, as in *Azeca tridens* (Pult.), *Clausilia laminata* (Mont.), etc.

FIG. 23—Example : *Azeca tridens* var. *nouletiana* Dupuy × 3, Lewes, Sussex, collected by Mr. T. S. Hillman.

TURBINATED, when the shell is of a conical shape, with a rounded base, as in *Limnæa stagnalis* (Linné), *Bythinia tentaculata* (L.), *Viviparus viviparus* (L.), etc.

FIG. 24.—Example : *Bythinia tentaculata* (L.) × 2, River Lea, Chingford, Essex, collected by Dr. R. F. Scharff, B.Sc.

CONTABULATE, when the shell is short, with shouldered or angulated whorls, as in *Limnæa stagnalis* var. *bodamica* Miller, *Physa fontinalis* v. *inflata* Moq., etc.

FIG. 25.—Example : *Limnæa stagnalis* var. *bodamica* Miller, Boden See, Switzerland, collected by Herr Schenk.

PATELLIFORM, when the shell is limpet-shaped or conical, as in *Ancylus fluviatilis* Müll.

FIG. 26.—Example: *Ancylus fluviatilis* Müll. × 2, Swarraton, Hants., collected by Rev. W. L. W. Eyre, M.A.

GLOBOSE, when the shell approaches a sphere in shape, as in *Helix granulata* Alder.

FIG. 27.—Example: *Helix granulata* Alder × 2, Ashley Downs, near Bristol, collected by Miss F. M. Hele.

TROCHIFORM, or CONOID, when the shell is conical, with a flattened base, as in *Helix terrestris* Pennant, *Hyalinia fulva* (Müll.), etc.

FIG. 28.—Example: *Helix terrestris* Pennant, Dover, collected by Rev. J. W. Horsley, M.A.

LENTICULAR, or LENS-SHAPED, when the shell is of a depressed form, with a more or less acute peripheral margin, as in *Helix lapicida* L.

FIG. 29.—Example: *Helix lapicida* L., St. Vincent Rocks, Clifton, near Bristol, collected by Mr. J. W. Cundall.

DEPRESSED, when the spire is only slightly raised above the body-whorl, as in *Helix itala* L., *Hyalinia nitidula* (Drap.), etc.

FIG. 30.—Example: *Helix itala* L., Tenby, S. Wales, collected by Mr. W. H. Boland.

DISCOIDAL, or QUOIT-SHAPED, when the shell has the spire flattened or even sunk in the centre, as in the *Planorbes*, *Valvata cristata* Müller, etc.

FIG. 31.—Example: *Planorbis corneus* var. *albina* Moq., Mill pond, Lifford, near King's Norton, Warwickshire, collected by Mr. J. Madison.

GIBBOUS, when the whorls are transversely swollen, usually near the aperture, as occasionally occurs in *Limnæa auricularia* (L.), *Limnæa stagnalis* (L.), etc.

FIG. 32.—Example: *Limnæa auricularia* var. *gibbosa* Taylor, pond, Moortown, near Leeds.

SCALARIFORM, when the whorls are almost separated from each other, as occasionally observed in *Helix pomatia* L., *Helix*

aspersa Müll., *Succinea putris* (L.), *Limnæa peregra* (Müll.), and many other species.

Fig. 33.—A Scalariform Helix.
Helix nemoralis monst. *scalare* Fér.,
Truro, Cornwall,
Collected by Mr. J. H. James, A.R.I.C.

Fig. 34.—A Scalariform Limnæa.
Limnæa stagnalis m. *scalariforme* Ckll.,
Pond, Chislehurst, Kent,
Collected by Prof. T. D. A. Cockerell, F.Z.S.

Ceratoid, or Scalarid, when the whorls are quite detached and separate from each other, often resembling a corkscrew, a ram's horn or a cornucopia, as occasionally found in *Helix aspersa* Müller, *Helix pomatia* L., *Planorbis umbilicatus* Müller, *Planorbis spirorbis* Müller, etc.

Fig. 35.—Example: *Helix aspersa* m. *cornucopia* Gmelin, garden of Mawnan Sanctuary, near Falmouth, collected by the late Rev. W. Rogers, M.A.

Fig. 36.—Female. Fig. 37.—Male.
Cyclostoma elegans (Müll.),
Yarmouth, I. of Wight,
showing the sexual difference in the tumidity of the whorls,
Animals dissected and the sexes verified by Mr. Chas. Ashford.

A Whorl is one complete spiral coil or volution of the shell, and the one completing the shell and ending at the aperture is termed the Body-Whorl; this is usually, but not invariably, the most capacious as well as the last formed, and in the diœcious species, as *Cyclostoma elegans*, is more tumid and voluminous in female than in male individuals. The whorls also vary in number in the different species, some, as *Vitrina*, *Testacella*, etc., having few and rapidly-enlarging whorls, while others,

Fig. 38.—A Paucispiral Univalve.
Vitrina pellucida v. *depressiuscula* Jeffr. × 2,
Haldon, Exeter,
Collected by Mr. E. D. Marquand.

Fig. 39.—A Multispiral Univalve.
Planorbis contortus (L.) × 2,
River Colne, Watford,
Collected by Mr. J. Hopkinson, F.L.S.

as the various species of *Planorbis*, etc., have numerous and more closely-coiled volutions. The whorls also exhibit peculiar characters

according to the species, showing great diversity in sculpture, colouring, and in the spinous, bristly or other appendages thereof. The various characters of the whorls may be designated as

STRIATE, when the parallel sculpture is fine and close; termed SPIRALLY STRIATE when the stronger lines revolve with the whorls, as in *Planorbis albus* (L.); and TRANSVERSELY STRIATE when they cross the whorls and are more or less coincident with the incremental lines of growth, as in the generality of the testaceous mollusca. Tryon and other authors term the spiral striation transverse or revolving, and regard the transverse striæ as longitudinal in character.

FIG. 40.—A Transversely and Strongly-Striate Univalve. *Helix caperata* Mont., Perth, Collected by Mr. Henry Coates.

FIG. 41.—A Spirally Striate Univalve. *Planorbis albus* (L.) × 3, Scout Dam, Penistone, Collected by Mr. L. E. Adams, B.A.

HISPID, or PILOSE, when the whorls are more or less densely covered with hairs, as in *Helix granulata* Alder, *H. hispida* Müll., etc.; or the hirsute appendages may be of a more downy character, as in the young of *P. corneus* (L.), etc., which are then termed PUBESCENT.

FIG. 42.—Example: *Helix granulata* Alder × 2, Ashley Downs, near Bristol, collected by Miss F. M. Hele.

CORONATE, when the spinous processes spirally encircle the whorls in a coronate form, as in *Helix aculeata* L.

FIG. 43.—Example: *Helix aculeata* L. × 8, Bassenthwaite, Cumberland, collected by Capt. W. J. Farrer.

MURICATE, ECHINATE, or SPINOSE, when the granulations or ribs upon the whorls are produced to a sharp point, as in *Planorbis nautileus* var. *crista* (L.).

FIG. 44.—Example: *Planorbis nautileus* var. *crista* (L.) × 8, pond, Roundhay, near Leeds.

PLICATE, or COSTATE, when the whorls are strongly ribbed or ridged transversely, as in *Helix pulchella* var. *costata* Müll.

FIG. 45.—Example: *Helix pulchella* var. *costata* Müller × 8, Pleshey Mount, near Chelmsford, collected by Mr. R. Miller Christy, F.L.S.

Sulcate, when the whorls are furrowed with comparatively wide groovings or channels, as in *Planorbis albus* var. *sulcata* Taylor, and *Helix rotundata* Müll.

Fig. 46.—Example: *Helix rotundata* Müller × 2, Hessle, Yorkshire, collected by Mr. J. D. Butterell.

Carinate, when the whorls are strongly and acutely keeled, the carination is most usually at the periphery, as in *Helix lapicida* L., and *Helix terrestris* Pennant.

Fig. 47.—Example: *Helix lapicida* L., St. Vincent Rocks, Clifton, near Bristol, collected by Mr. J. W. Cundall.

Cingulate, or Lirate, when the whorls are furnished with spiral ribs or ridgings, as in *Cyclostoma elegans* (Müll.).

Fig. 48.—Example: *Cyclostoma elegans* (Müller), Preston Candover, Hants., collected by Mr. H. P. Fitzgerald.

Decussate, Lacunose, Malleate, or Cancellate, when the spiral and transverse striæ or plicæ of the whorls form by their intersection a series of somewhat quadrangular and slightly hollowed areas; the intersecting lines form the style of sculpture termed Reticulate when they cross each other more or less obliquely.

Fig. 49.—Example: *Limnæa palustris* var. *lacunosa* Taylor, stream, Leventhorpe Pastures, near Leeds.

Varicose, when the thickening and sometimes consequent different colouring of the apertural margin, occurring in some shells, during rest periods in the process of growth, are not absorbed by the animal when growth is resumed, but remain crossing the whorls at regular or irregular intervals, as in *Limnæa stagnalis* (L.), *Helix nemoralis* L., etc.

Fig. 50.—Example: *Limnæa stagnalis* var. *variegata* Hazay, Peffer Burn, Luffness Links, Haddingtonshire, collected by Rev. Dr. McMurtrie, F.R.S.E.

The Umbilicus is the central cavity at the base of the shell and distinctly exists only when the columella is hollow, and is wide or contracted in correlation with the loose or constricted manner of

coiling ; when fairly developed so that one or more of the previous whorls are visible, as in *Helix itala*, the shell is said to be UMBILICATED ; if the orifice is small, as in *Helix granulata*, it is said to be

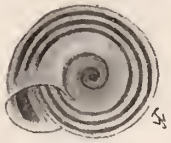


FIG. 51.—A Widely Umbilicated Univalve.
Helix itala Linné,
Royston, Cambs.,
Collected by Mr. H. G. Fordham.

FIG. 52.—A Perforate Univalve.
Helix granulata Alder × 2,
Mostyn, Flint,
Collected by Mr. W. D. Roebuck, F.L.S.

PERVIOUS or PERFORATE ; when very compressed, or a mere fissure, it is termed RIMATE, as in *Vivipara vivipara* (L.) ; but when the

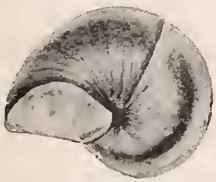


FIG. 53.—A Rimate Univalve.
Vivipara vivipara L.,
Canal, Marple,
Collected by Mr. William Moss.

FIG. 54.—An Imperforate Univalve.
Helix hortensis Müller,
Fordingbridge, Hants.,
Collected by Mr. H. Richardson, M.A.

columella is solid the shell is then called IMPERFORATE ; some species such as *Helix hortensis*, *Helix aspersa*, etc., are umbilicate or perforate when young, but at maturity become imperforate by the extension of the lip over the umbilical cavity (fig. 56).

The COLUMELLA, or PILLAR is the central portion or axis, real or imaginary, around which the whorls of the shell are coiled, but in very openly coiled or scalarid specimens the columella is only theoretically existent (p. 26, fig. 35). In the elongately spiral shells the columella, though always sinuous, may be nearly straight as in *Clausilia*, but in other cases, as in many *Helices*, it may be very tortuous and strongly twisted. Some species, as *Neritina fluviatilis* and *Carychium minimum*, absorb either wholly or in part not only

FIG. 55.—Section through the shell of *Clausilia laminata* (Mont). × 2, showing the nearly straight columella (from a section cut by Mr. F. Rhodes).

FIG. 56.—Section through shell of *Helix nemoralis* L., showing the somewhat twisted and hollow columella and the method of closure of the umbilicus at the maturity of the shell (from a section cut by Mr. F. Rhodes).

the columella but also the shelly partitions separating the coils of the body, so that in extreme cases the interior of the shell forms one simple cavity only, owing to this absorption of its internal divisions. Other species, as *Cæcilioides acicula*, *Testacella scutulum*, etc., have the columella truncate at its base; this peculiarity has been held to indicate carnivorous propensities in the species exhibiting it.

Fig. 57.—Univalve with Truncate Columella. *Cæcilioides acicula* (Müll.) ×6 Bishopswood, Ross, Herefordshire, collected by Rev. R. W. J. Smart, M.A.

Fig. 58.—Univalve with Elongate Spire. *L. glabra* (Müller), Twenty Pits, near Manchester, Coll. by Mr. J. R. Hardy.

Fig. 59.—Univalve with Depressed Spire. *P. corneus* v. *albina* Moq., Mill Pond, Lifford, near King's Norton, Warwickshire, Coll. by Mr. J. Madison.

The Spire includes the whole shell, with the exception of the last or body whorl, and is very varied in the character and disposition of its coiling. It may be discoidal or flat, as in *Planorbis*, or greatly elongated as in *Limnæa glabra*.

The Apex or nucleus of the shell originates in the ovum, and is the first and smallest whorl, and in some genera has great significance, being differently formed from the rest of the shell. In the elongately coiled species like *L. palustris*, the tip is liable to erosion and loss, the shell thus becoming decollate; the discoidal freshwater shells are not exempt from this injury, the *Planorbes* being found not unfrequently perforated through the centre on account of this erosion and loss of the earlier and smaller whorls.

Fig. 60. Univalve with Apex Perfect. *Limnæa palustris* Mull., Maidenhead, Berks., Coll. by Mr. C. G. Barrett.

Fig. 61. A Decollate Univalve. *Limnæa palustris* Müller m. *decollatum* Jeffr., Quarry, Christleton Rd. Chester, Coll. by Rev. H. Glanville Barnacle, M.A.

The Base of the shell is the opposite extremity to the apex: it is the anterior end and is the last formed part of the shell.

The Periphery is that portion of each whorl which is the most outwardly produced

Fig. 62. Basal aspect of an Univalve (slightly enlarged). *Helix hortensis* Müller, Fordingbridge, Hants., Coll. by Mr. H. Richardson M.A.

FIG. 63. — Univalve with Carinate Periphery. *Helix lapicida* L., St. Vincent Rocks, Clifton near Bristol, Coll. by Mr. J. W. Cundall.

and is usually medially placed between the suture and the base, following the spiral course of the volutions. In the carinate species, as *Helix lapicida*, the keel decisively indicates its position, and less strongly so when the keel is only faintly developed, as in *Helix caperata*, when the shells are termed sub-carinate or angulated; but in those species with regularly convex whorls, as *Helix nemoralis*, its precise position is more difficult to define.

FIG. 64. —Univalve with Sub-carinate Periphery. *Helix caperata* Mont., Perth, Coll. by Mr. Hy. Coates.

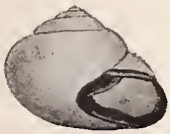


FIG. 65. — Univalve with Rounded Periphery. *Helix nemoralis* L., Isle of Lismore, Coll. by Mr. A. Somerville, B.Sc., F.L.S.

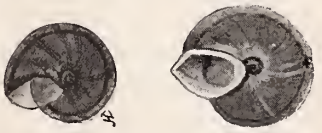
The SUTURE is the line of junction of one whorl with another, and varies in character and distinctness in accordance with the convex or planate outlines of the whorls. It may even be canaliculate or channelled, crenulated, or puckered, or simply more or less deeply impressed.

The APERTURE of the shell is the part last formed and is the opening through which the animal protrudes its body ; it may be almost exactly round, semi-lunar, or other shape, and is sometimes so greatly contracted with teeth or folds as to form almost a matter of surprise how the animal can insinuate its body through the constricted space.

FIG. 66.—Univalve with a Contracted Aperture. *P. antivertigo* (Dp.) × 20, Hemsworth, Yorks., Coll. by Mr. C. Ashford.

The PERISTOME or PERITREME is the margin of the aperture and may be distinctly continuous and detached during the whole life of the animal, as in *Cyclostoma elegans*, or only distinctly continuous and detached at maturity, as in *Helix lapicida* and in the *Clausiliæ*. It may however have the continuity of its outline and character broken by the penultimate whorl,

FIG. 67. — Univalve with Detached and Continuous Peristome. *Cyclos. elegans* (Müll.), Preston Candover, Hants., Collected by Mr. H. P. Fitzgerald.



FIGS. 68 & 69.—*Helix lapicida* L., Wells, Somersetshire, Showing the Continuous and Detached Peristome of Adult shell, and the Interrupted and Simple Peristome of the Immature stage. Collected by Rev. S. Spencer Pearce, M.A.

Fig. 70.—Univalve with Interrupted Peristome. *Helix nemoralis* L., Spurn Point, Yorks., Coll. by Mr. W. E. Clarke, F.L.S.

and is then termed "interrupted"; this separation is, however, only apparent, as the whorl is in all cases a complete tube, the penultimate whorl not forming the inner wall of the aperture, as has often been stated, but merely the foundation or support for the inner portion of the last formed whorl, thus enabling it to have the thinness and delicacy which usually characterizes it and has caused its existence to be overlooked or ignored. The left side which is so often closely appressed and adherent to the preceding whorl, is called the Inner or Columellar Lip, and also the Labium. Pfeiffer terms the portion of the aperture supported by the penultimate volution the Parietal Wall.

The Palatal Lip, Outer Lip, or Labrum, is the right side of the aperture in dextral shells and is usually thin and sharp in immature shells (p. 31, f. 68); but in some genera, as *Hyalinia*, it remains so in full-grown specimens, but generally it is thickened, expanded, or develops teeth-like folds, and other prominences at maturity (p. 31, figs. 66, 69).

Fig. 71.—Univalve with Simple Peristome. *Hyal. lucida* (Drap.), Torquay, Coll. by Mr. B. S. Dodd.

The Aperture has its length parallel with the length of the shell, and its width transversely to this; its many modifications in form and character may usually be ranged under one or other of the following heads, and is considered to be

Longitudinal, when its length is parallel to or coincident with the axis of the shell, as in *Limnæa stagnalis* (L.).

Fig. 72.—Example: *Limnæa stagnalis* (L.), Yardley Chase, Northamptonshire, collected by Mr. Lionel E. Adams, B.A.

Auriform, or Auriculate, when the aperture has approximately the shape or outline of the human ear, as in many species of *Limnæinæ*.

Fig. 73.—Example: *Limnæa auricularia* var. *albida* Jeffr., near London, collected by the late Mr. J. Pickering.

OBLIQUE, when it is produced more or less obliquely to the axis or columella of the shell, as in *Helix aspersa* Müller, *Helix nemoralis* L., etc.

FIG. 74.—Example: *Helix nemoralis* L., Bitton, near Bath, collected by Miss F. M. Hele.

COMPRESSED, when the aperture is diminished or compressed at the entrance, as in *Azeca tridens* (Pult.).

FIG. 75.—Example: *Azeca tridens* var. *nouletiana* Dupuy × 3, Lewes, Sussex, collected by Mr. T. S. Hillman.

CIRCULAR, when almost perfectly round, as in *Valvata piscinalis* (Müll.).

FIG. 76.—Example: *Valvata piscinalis* (Müller) × 3, Grantstown, Tipperary, collected by Mr. R. Rimmer, F.L.S.

LUNATE, when semi-lunar or semi-circular, as in *Hyalinia lucida* (Drap.).

FIG. 77.—Example: *Hyalinia lucida* (Drap.) slightly enlarged, Torquay, collected by Mr. B. Sturges Dodd.

ROUNDED, when not perfectly round, owing to the interruption by the penultimate whorl, as in *Helix pulchella* Müll.

FIG. 78.—Example: *Helix pulchella* Müller × 8, Kennington, Berkshire, collected by Mr. W. Whitwell, F.L.S.

TRANSVERSE, when its greatest extension is at right angles to the axis, as in *Helix lapicida* L.

FIG. 79.—Example: *Helix lapicida* L., St. Vincent Rocks, Clifton, near Bristol, collected by Mr. J. W. Cundall.

PYRIFORM, when the aperture is pear-shaped in outline, the compressed portion formed by the posterior sinus and the swollen part being at the anterior end, as in most species of the genus *Clausilia*.

FIG. 80.—Example: *Clausilia laminata* (Mont.) × 2, Winchester, Hampshire, collected by Mr. J. R. Brockton Tomlin, B.A.

PATULOUS, when the aperture is openly expanded, dilated or funnel-shaped, as in *Helix pulchella* Müll.

FIG. 81.—Example: *Helix pulchella* Müller × 8, Kennington, Berkshire, collected by Mr. W. Whitwell, F.L.S.

SINUOUS, when the outer margin is indented or sinuate in one or more places, as in *Vertigo antivertigo* (Drap.), *Vertigo angustior* Jeffr., etc.

FIG. 82.—Example: *Vertigo antivertigo* (Drap.) × 20, Hemsworth Dam, Yorkshire, collected by Mr. C. Ashford.

REFLECTED, RETUSE, or REVOLUTE, when the margin is folded or turned backwards, as in *Limnæa peregra* var. *labiosa* Jeffreys.

FIG. 83.—Example: *Limnæa peregra* var. *labiosa* Jeffr., Greenhead Park, Huddersfield, collected by Mr. J. Whitwham.

INFLECTED, or INVOLUTE, when the margin is folded or turned inwards, as in *Limnæa auricularia* var. *gibbosa* Taylor.

FIG. 84.—Example: *Limnæa auricularia* var. *gibbosa* Taylor, pond, Moortown, near Leeds.

DEFLECTED, when the aperture is bent downwards from the spiral line of coiling on the approach of maturity, as in *Helix itala* L., *Helix nemoralis* L., etc.

FIG. 85.—Example: *Helix itala* L., Tenby, S. Wales, collected by Mr. W. H. Boland.

DENTATE, when furnished with internal teeth or projections, as in *Pupa muscorum* (L.), *Carychium minimum* Müll., etc.

FIG. 86.—Example: *Carychium minimum* Müller × 16, Ceunant, near Welshpool, collected by Mr. J. Bickerton Morgan.

PLICATE, or LAMELLATE, when the internal folds or teeth become rib-like in character, as in *Pupa secale* Drap.

FIG. 87.—Example: *Pupa secale* Drap. × 4, Malling Hill, near Lewes, Sussex, collected by Rev. S. S. Pearce, M.A.

SEPTATE, when the interior of the whorls are contracted by projecting shelly processes, often leaving a tri-radiate opening for the mollusk, as in *Segmentina nitida* (Müll.).

FIG. 88.—Example: *Segmentina nitida* (Müller) × 3, Deal, Kent, collected by Mrs. Fitzgerald.

LABIATE, or MARGINATE, when callously thickened externally or internally at or near the margin, as in *Helix nemoralis* L., *Helix hispida* L., *Pupa muscorum* (L.), etc.

FIG. 89.—An Externally Marginate Univalve. *Pupa muscorum* (L.) × 6, Stivington, Northampton. Collected by Mr. W. D. Crick, F.G.S.

FIG. 90.—An Internally Marginate Univalve. *Helix nemoralis* L., Truro, Cornwall. Collected by Mr. J. H. James, A.R.I.C.

The LENGTH and HEIGHT of an ordinary spirally coiled Univalve shell are considered to be coincident and to be the distance from the base to the apex; some authors distinguish as simply the LENGTH, or HEIGHT, the distance between the apex and the base of the umbilicus, and regard the distance from the lower part of the aperture to the apex of the shell, as the TOTAL LENGTH; the BREADTH is the distance through or across the most ventricose part of the shell, parallel with the plane of the aperture, this being the maximum diameter, the line through the whorls at right angles to this, is the minimum diameter. The Patelliform *Ancyli* are usually considered to have their ALTITUDE or HEIGHT in the distance from the base to the apex or summit; their LENGTH in the distance from the anterior to the posterior margin of the aperture; and BREADTH in the distance from side to side.

The PELECYPODA or BIVALVES, also known as LIPOCEPHALA and LAMELLIBRANCHIATA, are exclusively aquatic mollusks, and differ markedly from the Gastropoda, not only in their shell, but in many points of their organization, and rank next that group in the number and variety of its species and genera, though individually the Pelecypods are relatively the most numerous.

The shells of Bivalves are typically composed of two distinct and convex or flatly conoid pieces or valves, which are applied to the right and left sides of the animal, and in the diœcious species, as in the univalves, the shells of female individuals are said to be noticeably shorter and more ventricose than those of the males.

The line along which the valves are joined together by the ligament is called the hinge-line, and is placed on the dorsal region of the animal, forming the UPPER or DORSAL MARGIN of the shell; the side opposite the hinge is the VENTRAL or LOWER MARGIN and is

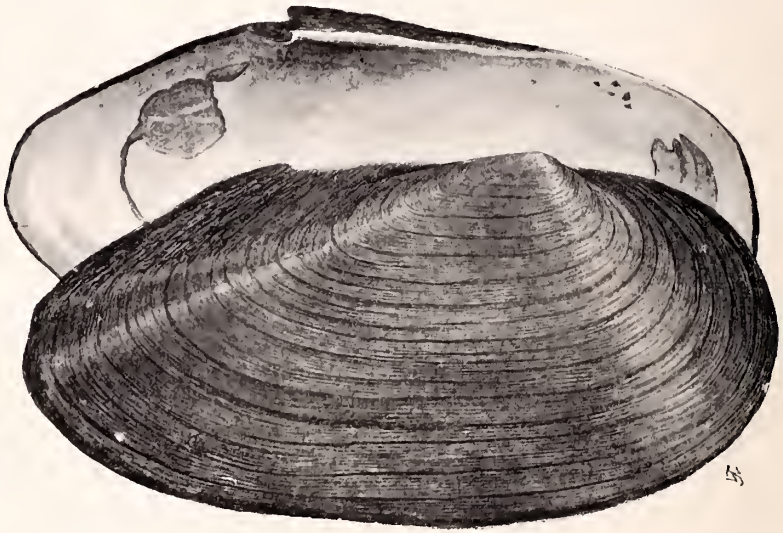


FIG. 91—An Equivalve Inequilateral Bivalve.
Anodonta cygnea (L.),
Clumber Lake, Notts., collected by Mr. C. T. Musson, F.L.S.
Showing the convex exterior of right valve with the lines of accretion or growth; and the concave interior surface of the left valve with the scars of the adductor and retractor muscles, etc.

always more or less thin and sharp; the end upon which the ligament is situated is the POSTERIOR or SIPHONAL MARGIN, the orifices of the branchial or incurrent and the anal or excurrent siphons being

placed there; the opposite end forms the ANTERIOR or CEPHALIC MARGIN, and is the end where the mouth of the animal is placed. The two valves are termed right or left, according as they are placed on the right or the left side of the animal, and are easily identified and discriminated; one method is to place the shell in its natural position as when the animal is crawling, with the ligament upwards and towards the observer, and the opposite or anterior end pointing forwards, in this position the right and left valves correspond to the right and left hand of the person examining it; or the separate valves can be distinguished by placing or holding the valve before you, with the inner surface upwards and the ventral margin toward you, if when in this position the ligament lies to the right, then the valve is the right valve, if to the left, the left valve; the functional ligament always being more or less posterior to the umbones, never anterior to them. Linné and many of the older naturalists described the ventral or lower margin of the shell as the top, the hinge-line as the base, and the left valve as the right, and *vice versa*. C. Pfeiffer and others follow Draparnaud in regarding the siphonal end as the anterior one, and as they consider the ventral margin to be the lower one, the right and left valves of these authors necessarily correspond with the left and right valves respectively of English conchologists.

The shells of the *Unionidæ* are like those of many Gastropods composed of three distinct layers; the outer layer or epiconch covers the external surface, and is reflected over the edge of the shell upon the free margin of the mantle, with which it is said to be organically connected. The middle or prismatic layer, according to Macalister, is absent in the shell of *Sphærium*, it is however present in the genus *Anodonta*, forming about half the thickness of its valves, and is composed of numerous polygonal prisms set obliquely to the surface of the shell and forming a very densely calcified layer; the nacreous layer is usually about the same thickness as the prismatic layer, but it is in this respect to a certain extent dependent upon and proportionate to the age of the animal, it lines the whole internal surface of the shell,

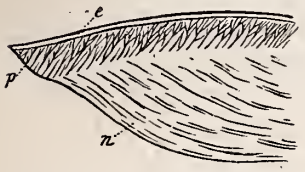


FIG. 92.—Oblique section through the shell of *Unio* (magnified), showing the three layers of which the shell is composed and the comparatively enormous development of the nacreous layer (after Semper).

e, periostracum or epidermis, the external layer; *p*. prismatic or middle layer; *n*. nacreous or inner layer.

except the free margin of the valves, being secreted by the whole external epithelium of the mantle, and consisting of a number of superimposed laminæ laden with calcareous particles, as many as twelve distinct laminæ were clearly separated in a valve of an apparently adult *Anodonta cygnea* from Burwell fish-pond, and we have possibly in this feature another indication of the age of the mollusk. In the genus *Unio* the prismatic layer is comparatively thin, while the harder and more compact nacreous or inner layer is very thick.

Though the shells of our Bivalves are approximately equal in thickness throughout their entire extent, yet at maturity there is in most species a noticeable submarginal thickening developed around the free edges of the valves, this thickening also occurs, though less markedly, at the termination of each seasonal or periodic stage of growth. Moquin-Tandon affirms that the Bivalves are thickest near the umbones, but although this may probably be the case in most species, and even also in the *Unionæ*, when under the stimulus of erosive action, they have abnormally and enormously thickened the umbonal region, by secreting additional layers of calcareous matter, as a protection against the destructive action of acidulous waters; yet usually the thickest part in those shells is the area on the anterior side near the ventral margin, and in position almost coincident with the anterior part of the pallial line and really forming part of the Ventral Crest of Picard, this thickened part is chiefly composed of the nacreous layer, the prismatic layer in the genus *Unio* having its greatest thickness, both comparatively and actually, at the posterior end of the shell.

The left valve of a specimen of *Anodonta cygnea* collected by Mr. W. D. Roebuck, F.L.S., in Burwell Fish-pond, near Louth, weighing 27·566 grams, was analysed by Mr. Crowther by the wet process—the same method as was adopted in the analysis of the shells of *Helix pomatia* and *Limnæa stagnalis*, the results of which were given at p. 20—and gave as a result 25·231 grams of inorganic, and 2·335 grams of organic substances, or 91·53 per cent. of inorganic earthy salts, and 8·47 per cent. of organic matter.

The right valve of another adult specimen from the same locality weighed 36·861 grams, and of this about one-third was analysed by the dry method, and burned to Calcium oxide, CaO, when the loss of moisture, organic matter, etc. was found to be 20·008 per cent.

The much greater difficulty found in dissolving the calcareous shell of *Anodonta*, than was experienced in dissolving those of *Helix pomatia* and *Limnæa stagnalis*, suggests the probability that the calcareous basis of the shell in *Anodonta* may be more especially composed of that form of carbonate of lime termed Aragonite.

Bivalves are mostly EQUIVALVE, the right and left valves corresponding with each other in form, size, etc., as in *Anodonta cygnea* and other species. All our fresh-water Bivalves are, however, strictly Equivalve shells, with the exception of *Dreissensia polymorpha* which is undoubtedly INEQUIVALVE, the left valve being somewhat larger than the right, and to some extent overlapping it near the acuminate umbones, and in addition to this disparity in size and shape, the byssal aperture or sinus is usually placed exclusively upon the right valve, though in some specimens the byssal opening modifies more or less unequally the shape of both valves and, in rare instances, that of the left valve only. Although our species are thus with one exception Equivalve, they are almost invariably and universally INEQUILATERAL or more or less unequal-

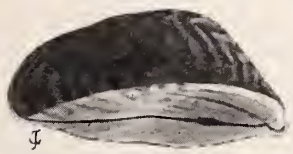


FIG. 93. — An Inequivalve Inequilateral Bivalve.
Dreissensia polymorpha (Pallas),
Baker's Dock, Stourport,
Collected by Mr. J. W. Williams.

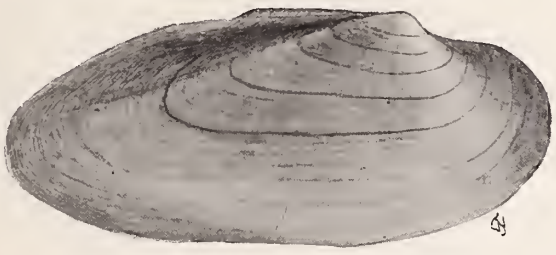


FIG. 94.—A Posteriorly produced Inequilateral Bivalve.
Unio pictorum (L.), right valve.
Hethersett Lake, near Norwich, collected by Mr. A. G. Stubbs.

sided, the umbo being placed towards one end, and the anterior side being usually the shortest, as in *Unio pictorum*, etc.; but this is reversed in *Pisidium*, as in many species of that genus, the posterior side is distinctly shorter than the anterior; this interesting structural difference can very easily be verified by observing the position of the ligament which in *Unio* will be found to be always at the

longer side and in *Pisidium* at the shorter end of the shell; this striking distinction was overlooked by Dr. Jeffreys, who, in his "British Conchology," erroneously described the posterior side of the shell of *Pisidium* as that most produced.

Fig. 95.—An Anteriorly produced Inequilateral Bivalve.
Pisidium amnicum (Müll.), right valve, × 2.
Canal, Ambergate,
Collected by Rev. H. Milnes.

When the umbo is situate about the centre of a symmetrically formed shell, so that the outline and area of the anterior and posterior sides correspond, the shell is called EQUILATERAL; some species of the genus *Sphærium* have almost equilateral shells.

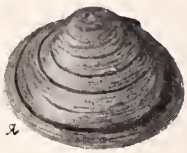


Fig. 96.—A Sub-equilateral Bivalve.
Sphærium rivicola (Leach), left valve, × 1½.
Canal, Northampton.
Coll. by Mr. W. D. Crick, F.G.S.

RENIFORM shells are often caused by some injury to the mantle margin, causing a deficient secretion at the injured part, and if this be along the ventral surface a more or less reniform or kidney-shaped shell results, the amount of sinuation depending upon the nature and amount of the injury sustained by the animal. The *Pisidium sinuatum* Bourg. is founded on a specimen of *Pisidium cinereum*

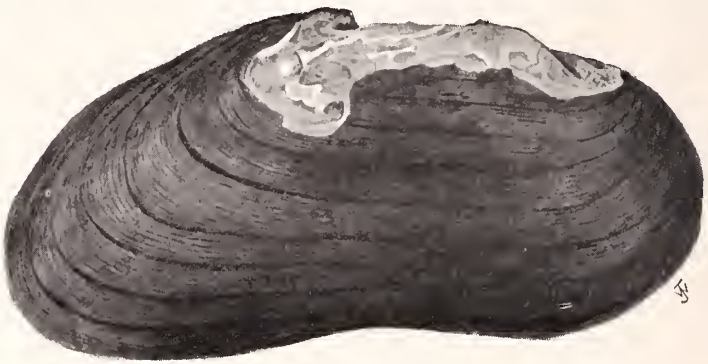


Fig. 97.—A Reniform Bivalve.
Unio margaritifer var. *sinuata* Lam., right valve,
Loch Awe, Argyleshire, collected by Mr. A. Somerville, B.Sc., F.L.S.

affected in this way. *Unio margaritifer* var. *sinuata* is an apparent example of this peculiarity of shape occurring normally, though Dr. Gray ascribes the form even in this case to the excoriation of the umbones. Mr. Madison has specimens of *Anodonta cygnea* which, owing to some injury, show this peculiarity in a very extreme form, the valves being quite cleft nearly to the umbones.

Symphynote or Connate shells are those in which the valves are united together along the dorsal margin, not only by the ligament but by continuous shell growth, thus forming a shell practically composed of a single piece. This is a character found more especially in *Anodonta*, but is confined to the juvenile stages of growth, at least in British specimens, the testaceous connection of the valves sooner or later becoming ruptured and broken by the opening and closing of the shell, and the connate peculiarity thus lost. Mr. Isaac Lea who so long and thoroughly studied the Naiads at one time attached great importance to this peculiarity and even proposed to divide them into two chief groups, according as they were or were not possessed of this character.

Fig. 98.—A Symphynote or Connate Bivalve.
Anodonta cygnea (L.), young, posterior end,
Grand Junction Canal, Brentford,
Collected by Mrs. Skilton,
Showing the testaceous junction of the two valves on the posterior dorsal margin.

Alate or "winged" shells are sometimes seen in some of the varieties of *Anodonta*; the alæ or "wings" being formed by a compressed upward extension of the posterior dorsal borders, sometimes exhibited in a very marked manner. This peculiarity is like the symphynotic, a characteristic, more especially affecting the juvenile life of species, at least in British specimens, gradually becoming less pronounced and striking as the animal advances in age and growth. The Symphynote and Alate characters are often combined together in the same individual, but this is not necessarily always the case.

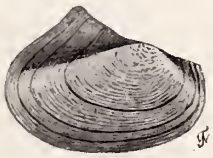


Fig. 99.—An Alate Bivalve.
Anodonta anatina (L.), young, right valve,
Canal, Apperley Bridge, Yorks.,
Collected by Mr. J. A. Hargreaves.

When the two valves fit accurately together at the margins, and appear to hermetically close the shell, as in *Sphærium corneum* and other species, the shells are called Close. If, however, owing to the margins of the shell not exactly coinciding with each other in shape or outline, the valves do not fit accurately together, and more or less visibly open spaces are left between the margins of the two valves for the protrusion of the

Fig. 100.—A "Close" Bivalve.
Sphærium pallidum Gray,
posterior end, × 2,
River Foss, Blue Bridge, York,
Coll. by Rev. W. C. Hey, M.A.

siphons, etc., as is the case to a limited extent in the Naiads, the shells are then called GAPING.

FIG. 101.—A "Gaping" Bivalve.
Anodonta anatina (L.),
Sandy bed of River Yare, Bramerton Wood-end, near Norwich,
Collected by Rev. S. Spencer Pearce, M.A.
g. gape of shell on the posterior dorsal margin, for the protrusion of the siphons; *u*. umbo or nucleus of the shell; *l*. ligament.

The UMBO (see fig. 101) is the prominent part or apex of each valve near the hinge, it is formed around the embryonic shell, which is the nucleus or apex of the umbo in each valve. They become wider apart with age and the growth of the shell, and are sometimes very different in character to the after-growth, as in *Pisidium henslowanum* and *Unio tumidus*, etc. In the different species of *Unio* the peculiar and remarkable undulation or sculpture of the umbones is becoming recognized and acknowledged as an important and reliable character, not only for the purpose of accurate specific discrimination, but also, for the arrangement of the species into natural groups, as this peculiar feature of the genus is said to be remarkably constant and less subject to modification than testaceous characters usually are. The umbones are always turned towards the anterior end, and in those foreign species with somewhat coiled umbones, the left valves

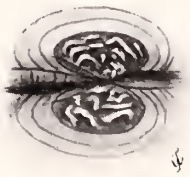


FIG. 102.—Umbones of *Unio tumidus* Phil. × 2,
Evesham,
Collected by Mr. J. Madison,
Showing the nodules and nodular ridges, characterizing the immature stage of growth.

FIG. 103.—*Pisidium henslowanum* (Shepp.), young, magnified (after Jenyns).
Showing the position and character of the peculiar eave-like projections in the young shell.

FIG. 104.—*Pisidium henslowanum* (Shepp.), adult, posterior end, × 12,
Pond, Cockerton, Darlington,
Collected by Mr. Charles Oldham.
Showing the greatly altered relative position of the umbonal appendages at the maturity of the shell.

bear great resemblance to the dextral shells of some gastropods, the right valve showing similar resemblance to sinistral forms.

FIG. 105.—A Caliculate Bivalve. *Sphærium lacustre* (Müll.), right valve, × 3, Pond, Sandal, Yorks., Collected by Mr. J. Hebden.

CALICULATION or Capping of the Umbones is apt to take place to a noticeable extent only in those species in which the embryonal shell is of a comparatively large size and somewhat globular shape and the succeeding shell-growth does not continue on the same plane, as is occasionally seen in some species of *Pisidium* and *Sphærium*.

The POSTERIOR and ANTERIOR CRESTS are most remarkably developed and most noticeable in immature shells, and mark off the posterior and anterior limits respectively, of the upper or dorsal margin; the posterior crest is sometimes distinctly and strikingly

FIG. 106.—A "Crested" Bivalve. *Anodonta anatina* var. *radiata* Jeffr., right valve, River Foss, Blue Bridge, near York, collected by Rev. W. C. Hey, M.A. Showing the anterior and posterior crests of the dorsal margin. *a.c.* anterior crest; *p.c.* posterior crest.

angulated in the adult shell of *Anodonta*, but in *Unio* the anterior crest is often the most strongly marked.

The ROSTRUM or BEAK is the produced posterior end of bivalve shells, and its extent is sometimes clearly defined on the posterior margin by two bluntly angular ridges—the most ventral one being the gonial ridge—which run towards the umbones. The term beaks has often been applied to the umbones, but should be discontinued to avoid the possibility of confusion. Dr. Brot who has especially

studied the Naiads, thinks the development of the rostrum is induced by agitated or running waters, but this is evidently not

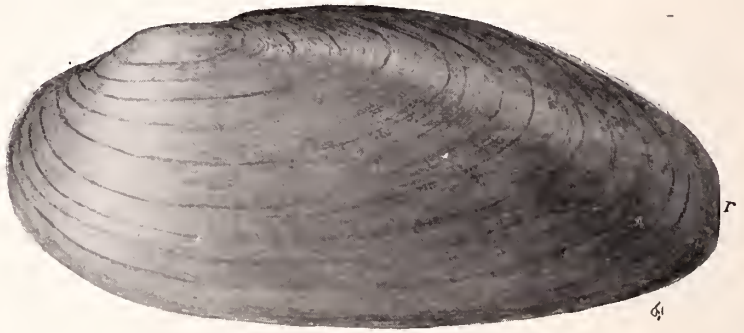


FIG. 107.—A Rostrate or Beaked Bivalve.
Anodonta cygnea var. *diminuta* Clessin, left valve,
Canal, Louth, Lincolnshire, collected by Mr. H. Wallis Kew, F.E.S.
r. the produced posterior end or rostrum.

the only predisposing cause, as the shell now figured was taken from the sluggish waters of the Louth canal, Lincolnshire.

The LUNULE is the oval or heart-shaped depressed space in front of, or anterior to, the umbones, and opposite to the ligament, and is sometimes defined by a more or less noticeable line. In the separated valves this space has been termed the ANTERIOR SINUS, and necessarily exists on both valves.

The ESCUTCHEON or CORSELET is the corresponding depressed space sometimes existing on the posterior dorsal or ligamental margin. In the separated valves it appears as an elongate space on each side of the ligament, and has been called the POSTERIOR SINUS.

FIG. 108.—*Anodonta anatina* v. *complanata* Rossm.,
Gumfrieston, near Tenby,
Collected by Mr. Fred. Walker.
Showing the position and aspect of the Lunule and Escutcheon. *lu*. lunule; *e*. escutcheon.

Moquin Tandon, the accomplished and accurate French conchologist, and many French and German authors, erroneously regard the lunule as the space posterior to the umbones, and the corselet or escutcheon as that anterior to them, a view diametrically opposed to that adopted by English and American authors. Draparnaud, who instituted the terms, clearly defines the position of the two areas, and establishes the accuracy of the English opinion upon this point.

The GONIUM is the lower posterior angle and the junction of the posterior and ventral margins; the GONIAL RIDGE is the elevated portion resembling an indistinct and blunt keel, extending from the

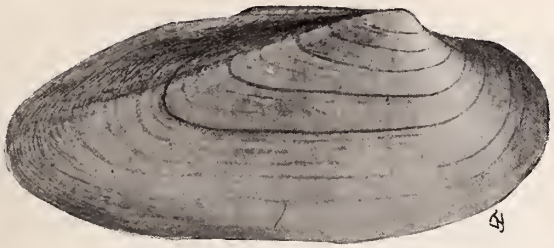


FIG. 109.—Bivalve showing Gonial Ridge extending from the Umbo to the Gonium, where the posterior and ventral margins join.
Unio pictorum (L.), right valve,
Hethersett Lake, near Norwich, collected by Mr. A. G. Stubbs.

Gonium to the umbo, and marking off the gonial area; it is sometimes very noticeable in *Anodonta* and *Unio*, and partly corresponds to the AREA of many authors.

The PODIUM is the lower anterior angle, and indicates the point where the anterior and ventral margins merge; the PODIAL RIDGE is the obsoletely angular line running from the umbo to the podium, and cutting off the podial area from the shell generally. It is strongly developed in *Dreissensia*.

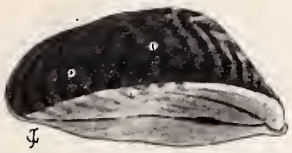


FIG. 110.—Bivalve showing Podial Ridge extending from Umbo to Podium at junction of anterior and ventral margin.
Dreissensia polymorpha (Pallas),
Baker's Dock, Stourport,
Collected by Mr. J. W. Williams.

The HINGE uniting the two valves of the shell is situate on the dorsal margin and is formed by the chitinous ligament and a more or less complicated series of denticles or teeth, which closely interlock with each other and would appear to function as a fulcrum in the opening and closing of the valves; the locomotive bivalves generally have the strongest and most powerful hinges, the sedentary and fixed forms usually having comparatively weak hinges and being sometimes quite edentulous.

The HINGE TEETH or DENTICLES are more or less complex, shelly, denticular processes or teeth, which with the ligament articulate the

shells. In young shells these processes or teeth are sharp and well defined, but in aged ones they often become thickened and their peculiar characters even obliterated by the continued deposition of shelly matter. These denticles are termed CARDINAL, or HINGE-TEETH when placed immediately beneath or between the Umbones, and ANTERO-LATERAL or POSTERO-LATERAL according as they are situate on the anterior or posterior side of the Umbones; these lateral teeth are generally distinctly lamellar in character, and sometimes very distinctly and strongly developed; these projecting shelly processes are generally arranged so as to fit between, and interlock with, corresponding cavities in the opposite valve. Occasionally the lateral teeth or denticles are developed and not cardinal ones, as in *Unio*, and shells with this type of hinge-teeth have been called Prionodesmacea by Dall, and Heterodonta by Neumayr; more frequently, however, in Pelecypods generally, the cardinal teeth alone are present. A formula has been devised for registering the different peculiarities of the hinge-denticles, the formula for the right valve being placed above, and that indicating the dentition

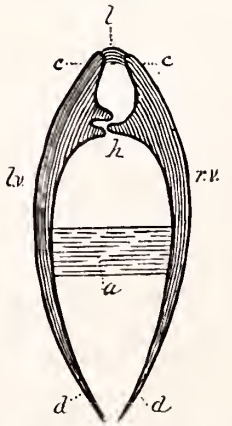


FIG. 111.—Diagram of a transverse section of the shell of a Bivalve (after Lankester), showing how the hinge teeth act as a fulcrum in the opening and closing of the valves.
a. adductor muscles; *l.* ligament; *r.v.* and *l.v.* right and left valves of the shell; *h.* hinge or fulcrum; *c.c.* the short arms of the lever; *d.d.* the long arms of the lever.

FIG. 112—Hinge-Teeth of *Unio tumidus* Phil. Groby Pool, Leicestershire, collected by Mr. H. E. Quilter.
a.l. antero-lateral lamellæ; *p.l.* postero-lateral lamellæ.

of the left valve beneath it, the cardinal denticles being first given, followed by the laterals, thus *Unio tumidus* could be recorded as Cardinal teeth $\frac{0}{0}$; Antero-lateral $\frac{1}{2}$; Postero-lateral $\frac{1}{2}$; which formula

indicates that the cardinal denticles are deficient in both valves, and that the right valve contains one antero-lateral and one postero-lateral lamella, the left valve containing two on each side, arranged so as to interlock with the lamellar ridges in the other valve; the anterior laminæ are always more or less crenate at their free margins and the more prominent and central denticle of the left valve is often distinctly bifurcate, as shown in the illustrative figure. Dr. Jeffreys was in error in his account of the denticulation of the hinge of the *Uniones*, ascribing the bidentate teeth to the right valve, which in normal shells has only unidentate lamellæ.

Sphærium rivicola may be considered to typify the shells possessing cardinal and lateral hinge teeth, both of are somewhat variable, in character. In well developed specimens the cardinal teeth are often distinctly double in both valves, the posterior cardinal tooth in the right valve, and the anterior cardinal tooth in the left valve, being larger than the other, often with a somewhat angular excavation and appearing as though formed by two converging denticles, their apices pointing to the umbo. In the unusually developed specimen from Leicestershire (f. 113), the cardinal denticles are more distinctly developed than is usual, and have a great resemblance to three more or less separate and converging shelly processes; the anterior lamellæ of the right valve are two in number, as in the normal shell, but in the left valve, a slightly developed additional lamella is perceptible nearer to the umbo and the outer shell-margin. The posterior lamellæ of the right valve have also developed an additional ridge also close to the outer margin and near to the umbo, affording a groove for the interlocking of the extra lamella appearing in the left valve; this specimen would appropriately be indicated by the formula, Cardinal $\frac{2}{2}$; Antero-lateral $\frac{2}{2}$; Postero-lateral $\frac{3}{2}$. In ordinary specimens the teeth may be formulated as Cardinal $\frac{2}{2}$; Antero-lateral $\frac{2}{1}$; Postero-lateral $\frac{2}{1}$; indicating that there are two cardinal teeth in each valve, and that the right valve contains two antero-lateral and two postero-lateral teeth, the left valve containing only one at each side interlocking

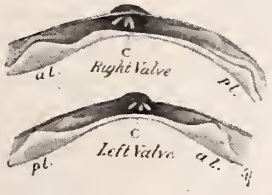


FIG. 113—Hinge-Teeth of *Sphærium rivicola* (Leach) × 4.
Canal, Blaby, Leicestershire,
Collected by Mr. H. E. Quilter.
c. cardinal denticles; *a.l.* antero-lateral lamellæ; *p.l.* postero-lateral lamellæ.

with the bifid laterals of the right valve, and thus offering a marked contrast to the denticles of the *Uniones*, in which this arrangement is reversed. Dr. Jeffreys, Reeve, and many other authors, have fallen into error on this point.

It should perhaps be mentioned that many continental and American conchologists regard the antero-lateral lamellæ of the *Uniones* as cardinal denticles, considering the antero-lateral lamellæ to be absent.

The Ligament is an uncalcified chitinous part of the shell usually

Fig. 114.—Bivalve with External Ligament.
Anodonta anatina (L.),
Sandy bed of River Yare, Bramerton Wood-end, near Norwich,
Collected by Rev. S. Spencer Pearce, M.A.
l. external ligament; *u.* umbo; *g.* gape.

attached to ridges along the dorsal margin, posterior to the umbones, and uniting the valves along the upper or dorsal margin. It is narrow, feeble and membranous, when existent anterior to the umbones, and is only functionally efficient and powerful posteriorly. It is large and strong in *Anodonta*, etc., but small in some marine genera which have a large internal cartilage between the valves. It is strong, brownish, convex, and very flexible during the life of the animal, but on its death becomes dry and brittle, though regaining some of its elasticity on immersion in water. The ligament is usually external, as in *Anodonta*, but is sometimes internal and lodged in a ligamental pit in each valve, as in *Dreissensia polymorpha*. When the valves are closed the elastic fibres forming the external ligament are stretched, but when the ligament is internal the fibres are compressed, the effect in both cases being the same, causing the valves to open as soon as the adductors are relaxed. The ligament is said to consist of two layers—an outer one, corresponding to the epiconch of the shell, and an

Fig. 115.—Bivalve with Internal Ligament.
Dreissensia polymorpha (Pallas),
Gloucester Canal, Stroud,
Collected by Mr. E. J. Elliott.
l. ligamental pit; *a.ad.* ant. adductor scar; *p.ad.* post. adductor scar; *p.r.* post. pedal and byssal retractor scar; *p.l.* pallial line.

inner portion, which combines two modes of striation, at right angles to each other, and giving the laminate appearance of nacre with the columnar appearance characteristic of the prismatic layer, and thus apparently showing the morphological and developmental similarity of the ligament and shell.

The EXTERNAL SURFACE of bivalve shells is generally more or less smooth, but all are marked by the successive growth-lines, which indicate the stages of increase in the size of the shell, as each of these lines was at one time the actual margin of the valve. The growth of a bivalve shell is not uniformly rapid in all directions, the rate of increase being most rápid towards the ventral and posterior margins, hence the umbo is always close to the dorsal margin and usually nearer to the anterior than to the posterior end; the incremental lines being more or less prominent according to the species. In some forms as *Pisidium amnicum* the shell is deeply and widely sulcate concentrically, while in others, as the various species of *Pisidium* and *Sphærium* the periostraca may be clothed with short, stiff, and more or less numerous microscopic hairs. Those on *Sphærium corneum* are short, thick, and somewhat bent at the points, somewhat sparingly distributed, but most numerous and thickly set near the umbones, and do not appear to be arranged in any set or geometrical order.

The INTERNAL SURFACE of the valves is ordinarily whitish, brilliant and often iridescent, but is sometimes delicately or richly tinted with salmon, rose, azure or other colour, and occasionally in some species is found of a deep livid blue or bluish-purple.

M. Picard has detected and recorded the presence of a broad ridge or thickened part of the shell in the interior of the *Uniones*, arising from the umbonal region and somewhat obliquely traversing the shell towards the ventral margin, this elevated area he has named the VENTRAL CREST, and the two divisions or chambers thus formed in each valve he has termed the ANTERIOR and POSTERIOR CHAMBERS respectively, according as they occupy the anterior or posterior end of the shell.

COLOUR is usually invested in the epidermis or periostracum, and is generally somewhat uniform, though of a stronger and richer tint towards the posterior end, the tinting being said to be greatly influenced by the nature and composition of the inhabited water, and to be more brilliant and elegant in still waters where there is a thick

layer of soft mud; in disturbed waters and on a different bottom the shells are usually duller in colour and often eroded at the umbones.

Diversity of Markings is not a striking character of British bivalves, the most remarkable example being furnished by the angular or zig-zag markings on the more exposed surface of the shell of *Dreissensia polymorpha*, the acutely angulated podial ridge forming a sharply defined boundary line, separating the distinctly ornamented posterior and general surface of the shell, from the plain and uniformly coloured anterior or podial area, from which the angular markings are quite absent.

Fig. 116. — Bivalve with Zig-zag Markings.
Dreissensia polymorpha (Pallas), Baker's Dock, Stourport, Collected by Mr. J. W. Williams.

The Radiate markings, so noticeable at times on the Naiads, are variable in colour, but are usually of some shade of yellow, brown, or green. They arise in the umbonal region, and are directed towards the free margin, but generally those rays which occupy the posterior

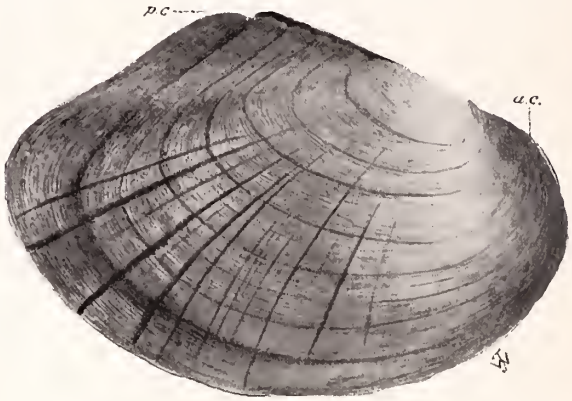


Fig. 117.—Bivalve with Radiate Markings.
Anodonta anatina var. *radiata* Jeffr., right valve, River Foss, Blue Bridge, near York, collected by Rev. W. C. Hey, M.A.

part of the shell, are more strongly coloured and more distinctly defined than those on the anterior part, which in the genera *Unio* and *Anodonta* is often more or less deeply imbedded in the sandy or muddy bottom of the lake or stream. These radiate and zig-zag markings are generally most vivid and distinct in immature shells, usually becoming more or less indistinct and obliterated by age.

The Concentric Zones, occasionally occurring in some species, sometimes offer a striking contrast of colours, especially amongst the species of the genus *Sphærium*. These comparatively broad and usually bright yellow zonal markings mostly occur only at the free margins of the valves, but at times they alternate at regular intervals with the normal greenish-brown ground colour of the shell, and have a pretty effect.

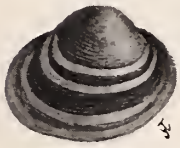


Fig. 118.—Bivalve with Concentric Markings.
Sphærium corneum var. *vittata* Garn., right valve, × 2, River Trent, Marnham, Notts., Collected by Mr. W. A. Gain.

In *Unio* and *Anodonta* these concentric zonal markings are generally darker in colour than the ground tint of the shell, in some cases being quite black; they represent according to Clessin the winter growth of the shell, and therefore indicate the age of the animal.

In Form, Bivalves are Oblong, when their length, or distance between the anterior and posterior margins, is greater than the width, or distance from the dorsal to the ventral margin, as in *Unio pictorum*, *Sphærium pallidum*, *Pisidium milium*, etc.; and termed Transverse, when the greatest length of the shell is in the opposite direction as in *Dreissensia*. The ordinary differences of form amongst our bivalves are not numerous and may be broadly classed as

Oval when the shell is of an oval form, as in *Sphærium rivicola* (Leach), *Pisidium pusillum* (Gmelin), etc.

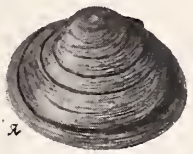


Fig. 119.—Example: *Sphærium rivicola* (Leach), left valve, × 1½, canal, Far Cotton, Northampton, collected by Mr. W. D. Crick, F.G.S.

Rounded when the shell has a somewhat circular outline, as in *Pisidium nitidum* Jenyns.

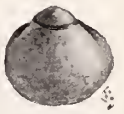


Fig. 120.—Example: *Pisidium nitidum* Jenyns, right valve, × 8, Hackfall, near Ripon, Yorkshire, collected by Miss Emily E. Harrison.

Oblong when the shell has its greatest length from the anterior to the posterior margins, as in *Unio pictorum* (L.), *Pisidium milium* Held., *Sphærium pallidum* Gray, etc.

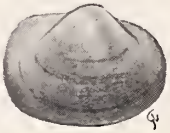


Fig. 121.—Example: *Sphærium pallidum* Gray, right valve, × 2, canal, Accrington, 1862, collected by Mr. R. Wigglesworth.

Triangular when the shell has a somewhat triangular outline, as in *Dreissensia polymorpha* (Pallas).

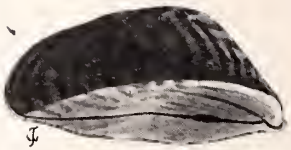


Fig. 122.—Example: *Dreissensia polymorpha* (Pallas), Baker's Dock, Stourport, collected by Mr. J. W. Williams.

Trapezoidal or Subrhomboidal when the shell is somewhat quadrilateral in outline and the opposite sides though somewhat straight, are not parallel, as in *Sphærium lacustre* (Müll.).

Fig. 123.—Example: *Sphærium lacustre* (Mull.), right valve, × 3, pond, Sandal, Yorks., collected by Mr. Joseph Hebden.

Compressed when the valves are flattened or compressed, the ventral margin forming a very acute angle, as in *Anodonta anatina* (L.), *Sphærium lacustre* var. *brochoniana* Bourg., etc.

Fig. 124.—Example: *Anodonta anatina* var. *complanata* Rossm., Gumfrieston, near Tenby, collected by Mr. F. Walker.

Reniform when the shell is oblong, but constricted near the centre of the ventral margin, forming a kidney-shaped outline.

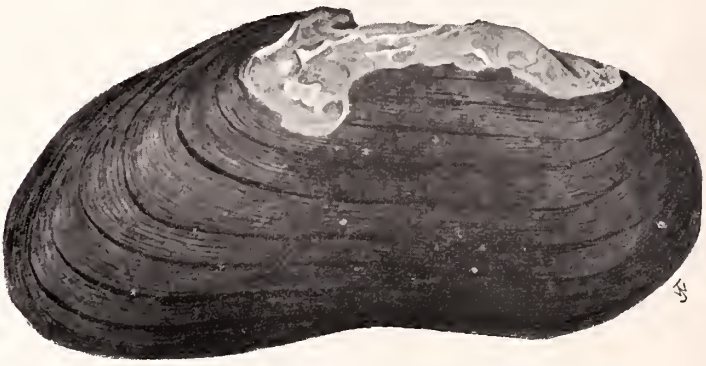


Fig. 125.—Example: *Unio margaritifer* var. *sinuata* Lam., right valve, Loch Awe, Argyleshire, collected by Mr. Alex. Somerville, B.Sc., F.L.S.

TUMID or CORDATE when the valves are very convex and swollen, often being somewhat heart-shaped in section, as in *Sphærium corneum* var. *nucleus* (Studer), *Anodonta cygnea* var. *cordata* Rossm., etc.

FIG. 126.—Example: *Sphærium corneum* var. *nucleus* (Studer), anterior end, × 2, ditch, Faversham, Kent, collected by the late Miss Fairbrass.

FALCATE when the shell though somewhat reniform in shape, has the produced posterior end greatly flattened, and somewhat curved.

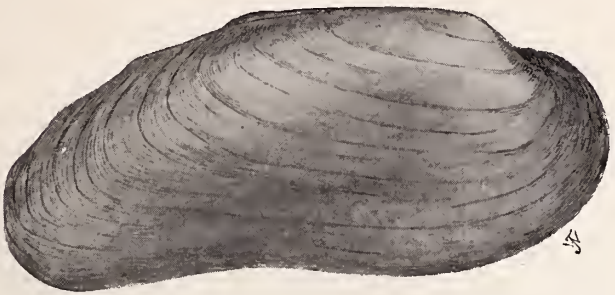


FIG. 127.—Example: *Unio pictorum* var. *platyrhinchoidea* Dupuy, right valve, River Yare, Bramerton Wood-end, Norwich, collected by Rev. S. Spencer Pearce, M.A.

TRUNCATE when the anterior or posterior margin of the shell, as the case may be, is not produced to a pointed end, but more or less abruptly terminated as in *Pisidium fontinale* (Drap.), *Unio pictorum* (L.), etc.

FIG. 128.—Example of a Posteriorly Truncate Bivalve. *Pisidium amnicum* (Mull.), right valve, × 2, Canal, Ambergate, Collected by Rev. H. Milnes, M.A.

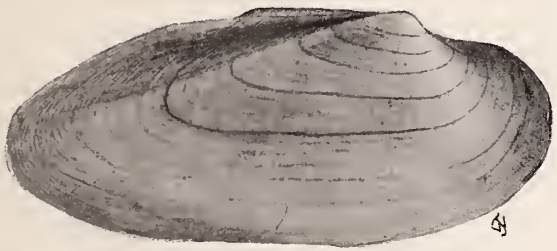


FIG. 129.—Example of an Anteriorly Truncate Bivalve. *Unio pictorum* (L.), right valve, Hethersett Lake, near Norwich, collected by Mr. A. G. Stubbs.

The Length of Bivalve shells, if the formation and disposition of the animal and its organs be accepted as guides, is the distance from the anterior to the posterior margins, not from the umbo to the front margin as proposed by Dr. Jeffreys, the oral extremity of the animal being placed at the anterior end of the shell, and the alimentary canal terminating near the posterior margin; the Breadth, is the diameter transversely to this, that is from the dorsal to the ventral margin — the length as proposed by Dr. Jeffreys; and the Thickness is considered to be at the greatest external convexity of the valves.

Muscular Impressions or Scars.

The more or less irregularly shaped and depressed muscular scars, or impressions, especially noticeable on the internal surface of bivalve shells, indicate the places where the muscles of the body are affixed to the substance of the shell and the points where the animal and shell are organically connected together.

In Gastropods, the columellar or retractor muscle, corresponding to the posterior retractor of the bivalves, leaves a double, or in some spirally coiled species, a single but not very conspicuous muscular scar upon the columella, about the distance of a whorl from the aperture. In *Helix pomatia* it is a fan-shaped or triangular impression, extending spirally round the columella for half a volution, its further margin being indicated by a slightly perceptible ridge, the acute angle of the cicatrix being directed basally, and its upper margin extending slightly upon the base of the preceding whorl.

Fig. 130.—*Helix pomatia* L., Nieder Kaufungen, near Cassel, Collected by Mr. P. W. Munn. Showing the character and position of the scar (*s*), indicating the point of attachment of the columella muscle (from a section cut by Mr. F. Rhodes).

In the Pelecypods, the principal muscular scars are the anterior and posterior adductor impressions. In *Anodonta cygnea* the anterior adductor scar is placed at the anterior end of the shell, the posterior adductor scar at about the same distance from the posterior margin, between the posterior end of ligament and the posterior margin of

the shell. The cicatrix of the anterior pedal retractor is contiguous to and joined with the anterior adductor impression, at its upper margin. The impression of the anterior pedal protractor is much smaller than that of the anterior adductor scar, and is placed posteriorly and ventrally to it. The posterior adductor impression is joined at its upper angle to that of the posterior pedal retractor. In addition to these, the more distinct marks of muscular attachment, there are a limited but variable number, of much smaller muscular pits in the umbonal region, about equally distributed in size and number upon the anterior and posterior sides of the umbones, and not always exactly corresponding either in number or position in the two valves, marking the points of attachment of several retractor or retentor muscular fibres.

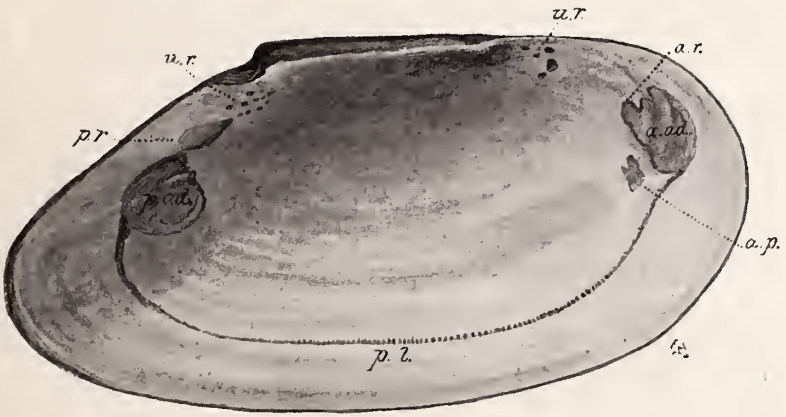


FIG. 131.—*Anodonta cygnea* (L.), left valve,
Clumber Lake, Notts., collected by Mr. C. T. Musson, F.L.S.
Showing the character and arrangement of the muscular scars.
a.ad. anterior adductor scar; *p.ad.* posterior adductor scar; *a.r.* anterior pedal retractor scar; *p.r.* posterior pedal retractor scar; *u.r.* umbonal or lesser retractor or retentor scars; *a.p.* anterior pedal protractor scar, the abdominal retentor scar of Clessin; *p.l.* pallial line.

Moquin-Tandon asserts that the anterior adductor impressions are always less-marked than those of the posterior adductors, this is however incorrect, as the anterior adductor impression, especially in *Unio,* is usually much more deeply and distinctly impressed than the posterior one, which, though somewhat larger in extent is not nearly so distinctly and strongly defined.

All these marks of muscular attachment become further apart and more distant from the umbonal region as the growth of the shell proceeds, and in some cases it is possible to trace faint and gradually

narrowing impressions from the margins of the present scars, converging towards the umbones, and showing the process of growth and the successive shiftings of the muscles.

The Pallial-line, which in the Integripalliate species follows more or less the outline of the ventral margin of the shell, is caused by the impressions of the points of attachment of the muscular fibres of the mantle, and indicates the line of attachment of the mantle to the shell. The siphonal impression or pallial sinus only exists in those shells with long and retractile siphons, its depth being an index of their length; the small siphons of *Sphærium* cause little or no inflection of the pallial-line.

Species.

Prior to the enunciation of the doctrine of evolution, the definition of species was simple and clear, as they could be described as the whole of the individuals descended from the pair originally created; the general organization and form of each species being considered to be immutable and as fixed by the Creator. The universal acceptance of the principles of evolution compel us to regard species as mobile and plastic, and although their characters may be modified by the responsive reflex action of the organism adapting itself more or less readily to the varying conditions of the environment, yet for all practical purposes specific characters can be regarded as stable and fixed, as any radical structural changes induced by the action of the different agencies of the environment, require lengthened periods to modify a sufficient bulk of individuals to firmly establish permanent and sufficient differences for specific distinction.

A species, therefore, may now be defined, as all the individuals which bear such resemblance, not only to their parents and offspring, but to each other, as to make it reasonably certain that they belong to one common stock. This assemblage of individuals should also be capable of inter-breeding amongst themselves, produce fertile offspring, and should not be too closely connected by intermediate forms with other species or groups of individuals.

The general form of the shell, and the arrangement and peculiarities of the sculpture and colouring furnish the principal testaceous characters of species in the Gastropoda; in the Pelecypoda, the different forms of the shell, the position of the umbones, the char-

acter of the hinge, etc., are all important features in the discrimination of species; the anatomical criteria differ in different groups, but in the Gastropoda reliable features for the differentiation of species are often found in the modifications of the different parts of the reproductive system, etc.

Some species are remarkably constant and more persistent in the retention of their characters than others; these inflexibly organized forms do not readily accommodate themselves to, or vary in response with the special nature of the environment, and are usually restricted in their distribution and difficult to acclimatize; according to Dr. O. Boettger, species of this character are ancient forms, which have existed from tertiary times, and are found fossilized in the deposits of that period, possibly these species have passed through their period of variability or specific youth, and have entered upon the period of decadence preceding their final extinction.

Others species are remarkably variable, and readily and quickly modify and adapt themselves to any change in their locality or surroundings; species of this character are according to Dr. Boettger, of comparatively modern origin, and are not found fossilized in the deposits of tertiary age and have therefore been presumably evolved from some pre-existing form since that period, the exuberant variations in form, size, colouring or texture they exhibit, are possibly evidences of their recent evolution and the youth of their specific life.

The opinion has within recent years gained ground amongst scientists in this country, that unless closely allied forms present some *internal* organic difference, they cannot rank as species. This, in my opinion, though an undoubtedly true and scientific test, should yet be applied with judgment and discrimination and not indiscriminately applied to every case, as the shell is just as truly an organ of the animal as the penis, spermatheca, dart, or buccal armature, and this being so, the shell becomes a valid criterion of difference, the only criterion if other sufficiently distinctive organic modifications are absent. If this is not so, then to be consistent we must unite under one specific name such forms as *Helix hispida* and *Helix rufescens*, as the chief differences between these species are testaceological rather than anatomical. Even Simroth with his vast experience cannot really decide, whether in certain genera of slugs, the external or internal characteristics possess the greater specific value and constancy.

The elevation of variously modified forms, and also those of a doubtful or transitional nature to specific rank, as is unfortunately the practice with some of the most able and acute continental conchologists of the present day, is earnestly to be deprecated. The treatment of these forms as varietal would sufficiently accentuate any differences they might possess, and yet fully preserve the necessary indication of their specific affinities; this object our gifted continental friends seek to attain by adopting a system of grouping, which groups are, I believe, nearly if not quite, co-ordinate with the old Linnean and Lamarckian species, thus the group *Stagnaliana* would in England be considered to be practically synonymous with the Linnean species *Limnæa stagnalis* and the different forms composing that group, would be, to our English views, simple varieties of that species. This unfortunate practice of multiplying species upon the slightest and most insufficient characters, cannot fail sooner or later to bring about a reaction, and thus cause more attention to be directed to the common, rather than to the divergent characters of species.

Varieties.

The tendency of offspring to resemble their parents is undeniable, yet no two children or organisms are exactly like each other, or like their parents in every particular, owing to being differently affected individually by the pre-natal as well as the post-natal environment, and diverging correspondingly from the likeness of their progenitors; these divergent forms are called

Varieties, and have been well defined as incipient species; marked divergence has begun, which may under favourable circumstances culminate in the evolution of distinct species. Varieties rank next in importance to species, and in accordance with their greater or lesser divergence from the typical form, have been subdivided and designated by various subsidiary names, intended to convey the relative degree of modification they have undergone.

Varieties may be individual, that is, occurring only in a more or less isolated and sporadic way; or, they may be of a sexual character, as in the diæcious species of both Univalves and Bivalves, in which the shells of the female individuals are generally characterized by a more obese and tumid form than those of the males. The peculiarities distinguishing varieties may also be acquired during growth,

owing to the deferred development of some of the organs of the animal, or other causes, as in those specimens where banding or other ornamentation, though not present in the early or youthful stages, become gradually developed and intensified as growth proceeds; or the change from the parental characters may be the apparently direct result of external causes, as has been demonstrated by Herr Hazay, who has developed the short-spired globose form of *Limnæa peregra* from the ova of the elongated typical form of the species, and *vice-versa*, according as the ova were placed and reared in still pools, or in "hard" running waters.

If the circumstances favouring certain variations be practically of a permanent character, and affect the bulk of the individuals of a species throughout a whole district, as may be the case where the apparent determining causes are physical or climatic, or as they have been termed Ectergogenetic, the modified form becomes hereditary and is then termed a SUB-SPECIES, GEOGRAPHICAL VARIETY, or RACE. These geographical varieties often have many of the characteristics of good species, possibly as a consequence of long isolation from the typical form, and they cannot always with certainty be specifically determined, even after an examination of the structure of the animal; thus according to Simroth the species of the genus *Amalia* are very unstable, each country impressing its own local stamp upon the species inhabiting it, and the majority of forms set up as distinct species by various authors are only transition forms bridging over the interval between *carinata* and *sowerbyi* on the one hand and *carinata* and *gagates* on the other. Some species and genera are however less subject to variation than others, and these groups or species showing least adaptability to modified circumstances are usually more or less restricted in their distribution.

The term VARIETIES when used in a restricted sense, refers to individuals which have developed or acquired very noticeable differences from the typical or parent form, but have not occupied any special district to the virtual exclusion of the type, but coexist with it, being more sporadic and isolated in their occurrence, possibly owing to the predisposing causes being of a limited or evanescent nature, or perhaps intrinsic to the individual, and not therefore of so general and pervading a character as is the case where the mass of the individuals inhabiting some definite area are affected, as in the geographical varieties.

The mere number of individuals affected should not however lessen the interest and scientific value of the differences exhibited, as there must always of necessity be a full and sufficient predisposing cause which it should be our aim to discover.

The internal organs of the animal are also equally subject to modification, and it is quite conceivable that anatomical differences might arise which would have an important bearing on the origin of specific differences, a modification of the sexual system might debar or restrict intercourse with individuals of the species not similarly affected, and thus pave the way to further and permanent modification. This aspect of the subject which has been termed Entergogenesis, has not received much attention up to the present time, so that it is not at all certain, whether the internal change may not often be the prior one, in the evolution of new and distinct species, as Eimer from his observations on colouring considers that species mainly originate from variation due to constitutional causes.

From whatever causes induced these modified and modifying forms are of the highest interest and importance, as exhibiting in actual progress the processes of differentiation which may ultimately lead to the evolution of distinct species, it is therefore very desirable that well-marked variations exemplifying the various lines of divergence should be designated by a distinct and preferably conventional varietal name. The adoption of this practice will undoubtedly facilitate their study, though it is seldom desirable to attach special and distinctive names to the intermediate forms connecting the extreme varieties with each other or with the parent form. These intermediate as well as the complex forms might where and when desirable be distinguished by a judicious though temporary combination of names already applied, thus if it were wished to mention from any cause a specimen exhibiting a colour-variation in combination with another peculiarity, its character could be concisely indicated by combining the names of its chief modifications; a sinistral *Limnea peregra* if also an albino would be alluded to as *sinistrorsum-candidum*, and so on in other cases without however listing the names.

The term Sub-variety or Mutation is used when referring to the slighter modifications either of the typical shell or of the varieties, they are really the intermediate forms which connect and blend together the well-marked varieties with each other and with the

typical form, and therefore possess a certain value and importance, as enabling or assisting us to fix the varietal status, and refer to their appropriate species, the doubtful and abnormal forms occasionally met with; but the relative importance of the varietal or sub-varietal modifications cannot always be measured in accordance with the more or less readily discernible nature of the differences exhibited. The conspicuous differences in the variations of the banding of the shells of *Helix nemoralis, Helix hortensis* and other Pentateniate species, although palpable and unmistakeable to the most unpractised eye, are relatively of very minor importance, in comparison with the more subtle variations in form or character, which may often require a trained eye and judgment to discern and appreciate; the variety *lutea* of *Helix hortensis* strictly speaking refers only to the bright yellow shells, though generally understood to include all yellow forms, and these can and have been sub-divided and named by different authors, the greenish-yellow form has received the names of *flavo-virens* from Picard and *flavo-viridis* from Kickx, the greyish-yellow forms have been styled *griseo-lutea* by Esmark, and all the innumerable band modifications whether of number, color, or arrangement are sub-varieties or modifications of the more important varieties.

The Depressed and Conoid forms of species usually somewhat subglobose in shape, results from a more or less rapid deflection of the whorls; if, in the process of growth, the whorls descend more quickly than usual, we have as a result a more produced and elongated form of shell with a smaller aperture, as in *Helix nemoralis* var. *conica*

Fig. 132.—A Conical variety of a Subglobose Univalve.
Helix nemoralis var. *conica* Pascal, Seacroft, near Leeds.

Fig. 133.—A Depressed variety of a Subglobose Univalve.
Helix nemoralis var. *planospira* Picard, Frutigen, Switzerland.

Pascal. Inversely, if the descending growth of the whorls be less decisive than normal, then we have a depressed and more or less planorbiform shell, as in *Helix nemoralis* var. *planospira* Picard, and this form of modification usually results by correlation of growth in a shell of greater diameter than ordinary with a more expanded aperture.

Land shells of elongate form, are often somewhat arboreal in habit or at least more inclined to ascend to elevated positions, than the flat spired forms, which would appear to be in many cases more geophilous, or ground-loving in habit; our most depressed species, *Helix obvoluta* is particularly noticeable for this peculiarity, naturally there are exceptions to this rule, which however indicates in a general way the tendencies of the various forms.

Fluviatile species tend to develop a lengthened shell under the influence of a steady and rapid current, and short spired forms, of otherwise elongate shells, more or less characterize species inhabiting lakes and other large bodies of water, *Limnæa peregra* var. *burnetti* and *Limnæa stagnalis* var. *bodamica* may be instanced as exemplifications of this rule, and, as recorded at page 59, Herr Hazay has produced the long-spired variety of *Limnæa peregra* at will from the ova of the globose form by merely rearing them in a rapid current of water.

Fig. 134.—A Short spired variety of an elongated Univalve.
Limnæa stagnalis var. *bodamica* Miller,
Boden See,
Collected by Herr Schenk.

In the Pelecypods the shape may be modified by the greater or lesser convexity of the valves, which may be considered analogous to the conoid and depressed varieties in the Univalves. In those species

Fig. 135.—*Unio tumidus* Phil.,
Groby Pool, Leicestershire, collected by Mr. H. E. Quilter.
Showing a regularly inflated burrowing Bivalve, usually characteristic of still waters
(this specimen shows the peculiarity of three distinct and successive margins to each valve).

which do not regularly imbed a portion of their shells in the bed of the stream or pond, the tumidity or compression of the shell is somewhat uniform over the whole shell, but in the species composing the genera *Anodonta* and *Unio*, which usually live partly buried in the

bed of the river or pond, the effects of the special features of their environment are shown more particularly at the posterior or siphonal end of the shell, which is fully exposed to such modifying influences as may exist. In still pools, lakes, or slowly flowing waters the shells of these genera may be more or less equally inflated, resembling in this respect those species which do not partially imbed their shells in the muddy bottom of the water. In rapidly flowing streams and rivers the shells are often specially characterized by a remarkable compression and extension of the posterior end, as in *Unio pictorum* var. *platyrhinchoidea* Dupuy—of which Dr. Jeffreys' var. *compressa* is a sub-variety of somewhat broader form and slightly less sinuate lower margin—this remarkable variety was originally discovered in

FIG. 136.—*Unio pictorum* var. *platyrhinchoidea* Dupuy,
Hethersett Lake, near Norwich, collected by Mr. A. G. Stubbs.
Showing a compressed burrowing Bivalve, usually characteristic of flowing waters.

this country by Mr. Bridgman in the River Wensum, near Norwich, which is a slow and sluggish stream with a layer of soft mud over a hard bottom ; the particular parts inhabited by this peculiar variety are the places where the river bends sharply and forms what are locally called "horse-shoe reaches," the current rushing rather sharply at the last bend to the opposite bank and forming an eddy next the shore, the rush of the current removing all the loose soft mud covering the hard bottom. These remarkable shells are found burrowing in the hard ground just inside and at the edge of the sharp current, next to the eddy, and are assumed with great probability to be an effect of the rush of the current and the consequent washing away of the softer river bed, rendering it more difficult for the mollusk to imbed its shell, this process being, however, probably facilitated by the more blade-like character of the shell generally, the broader valves when firmly imbedded preventing the mollusk being washed from its position too easily, and as the thin dorsal posterior edge of the shell is presented to the current, there is less friction to overcome. It is, however, very remarkable

that the fine specimen figured is from a lake near Norwich; possibly there may be some special features in the locality, or of its occurrence there that would explain the seeming anomaly of its presence in still waters. In the variety *ovalis* of *Unio tumidus* the same peculiar compression of the posterior margin is exhibited, but the shell is somewhat inequivalve, the left valve being slightly concave on the posterior end, while the posterior end of the right valve is convex in even a greater degree. These and other results of environment tend to give a general local likeness to allied species inhabiting the same river or lake—a fact which has often been noted and commented on.

FIG. 137.—*Unio tumidus* var. *ovalis* (Mont.), River Frome, Stapleton, Bristol, Collected by Miss F. M. Hele.
Showing the compressed and somewhat curved posterior margin, and the slightly unequal valves.

The GIBBOSITY which some species occasionally form by abruptly enlarging and afterwards contracting the diameter of the whorls, is very curious, and the suggestion has been made that a temporary accession of nourishing and palatable food during the growth period, would on account of the suddenly increasing bulk of the animal necessitate the unusual enlargement. Should this unusual food-supply become exhausted, or not easily obtainable, the proportions of the animal would become gradually reduced to the normal size and the shell more or less quickly contracted in correlation with it.

FIG. 138.—A Gibbously Inflated Univalve.
Limnæa auricularia var. *gibbosa* Taylor, Pond, Moortown, near Leeds.

Mr. R. E. C. Stearns ascribes analogous bulgings in the American *Planorbes* merely to the periodicity of growth, owing to recurrent periods of hibernation, the termination of each growth period being marked by an expansion of the aperture, which may be considered analogous to a varix, and the repetition of these varical enlargements give the American species their special feature. The habit of forming these enlargements would be continued for a period, even though the species had migrated to districts where owing to more equable conditions hibernation was unnecessary, though in time they would revert to producing an even and regular growth.

This transverse bulging of the whorls during the course of growth is occasionally observed in a pronounced form in many species, especially in *Limnæa stagnalis*, and would appear to be a very general outward biological expression of a number of abnormal conditions, as well as of a period of superabundance of nourishing and palatable food. In the autumn of 1894 all the specimens of *Limnæa stagnalis* found in a small pond at Osmondthorpe, near Leeds, exhibited this remarkable inflation upon the body whorl, but those gathered during 1895 in the same place did not show the peculiarity, so that the cause of the expansion, whatever may be its nature, was evidently an evanescent one. The pond has a rich and varied vegetation and contains many forms of animal life, and it may be remarked that leeches, which Herr J. Hazay states are sometimes the cause of whorl expansion, were numerous in it. The very interesting specimen of *L. stagnalis* var. *bodamica*, which I owe to the kindness of Mr. Brockton Tomlin, also shows this peculiarity in a very striking manner.

FIG. 139.—An Univalve with Gibbously Inflated body whorl. *Limnæa stagnalis* (L.), Pond, Osmondthorpe, Leeds, Collected by Mr. H. Crowther, F.R.M.S.

Identical inflated growths are occasionally developed by specimens in confinement, and Mrs. Skilton has kindly furnished me with a characteristic sketch of a specimen of *Limnæa stagnalis* reared in her aquarium, which distinctly shows this remarkable whorl distension.

FIG. 140.—An Univalve with Gibbously Inflated body whorl (dorsal aspect). *L. stagnalis* v. *bodamica* Miller, Boden See. Collected by Herr Schenck.

The Pelecypods, more especially *Anodonta cygnea*, are liable to a similar inflation, though less markedly so than the Univalves; this gibbous swelling, when it does occur, is naturally of a concentric character, in harmony with the lines of growth or increase.

The various LABIATE or lipped forms have had several theories advanced to account for their peculiarities. In some cases the suggested explanation of the origin of the gibbous varieties may to some extent apply to this deviation also, and if so the determining circum-

stances would occur later than in the gibbous variety, and only just prior to the final completion of the shell. Although the majority of known specimens showing an expanded lip are from tranquil waters, yet this peculiarity has been assumed to be also the result of the animal living in turbulent waters, compelling it to cling closely to stones, etc., to avoid being detached and washed away. An analogous cause suggested by several observers is that it may be a consequence of the animal being compelled to reside mainly upon and crawl over flat and hard surfaces during the growth period, as upon tank sides in captivity, or upon the hardened mud of ponds which have become partially dried up.

Fig. 111.—An Univalve with Reflected lip.
L. peregra v. *labiosa* Jeffr. × 2, Greenhead Park, Huddersfield, Collected by Mr. J. Whitwham.

Expanded or reflected lip growth has however often been observed to occur during the autumn when the reproductive season has terminated and the cessation of this drain upon the system enables the food consumed to contribute solely to maintain and increase the bulk of the animal and may thus necessitate an expansion of the shell; but the enlargement may also occur at the normal growth period, if suitable food be abnormally plentiful and ethological conditions favourable to such increase.

Fig. 112.—An Univalve with Expanded lip.
Limnæa stagnalis (L.), Ashton-under-Lyne, Collected by the late Mr. Lister Peace.

The Armature of the aperture or mouth of the shell is a feature which is usually the attribute of the perfectly adult state. Some species, as *Vertigo minutissima*, may exist in our own country in a perfectly edentulous form, which in other countries develop a varying number of denticles contracting

Fig. 113.—*Pupa secale* Drap. × 4, Malling Hill, near Lewes, Collected by Rev. S. S. Pearce, M.A.,

Fig. 114.—*Pupa secale* var. *edentula* Taylor × 4, Ingleton, Yorks.,

Showing the typical form and a perfectly edentulous variety of a normally strongly dentate or plicate species.

the aperture of the shell. Others, as densely denticulate as *Pupa secale*, vary in the number of teeth possessed by the mature shell, and may even have a variety in which the whole of the denticles contracting the aperture have become obsolete.

An interesting variety of *Hyalinia fulva*, if the identification be correct, is recorded from Cincinnati, U.S.A., in which the immature shells develop within the interior of the last or body whorl, a number of little denticles, radiating from the umbilicus like the spokes of a wheel, approximating in this respect to the character of *Gastrodonta*, of which genus several species are found in that region. This peculiarity, which disappears in the adult, is said to be a probably defensive provision against a small tender grub, which lives in beds of leaves and preys upon small mollusks. These structures are quite analogous with the denticles and folds found in the post-embryonal *Pupa cylindracea* and *Pupa anglica*, which also in a great measure disappear at maturity, and are thus a character especially distinguishing the juvenile stage of growth.

FIGS. 145 & 146.—*Pupa anglica* (Fér.) × 12,
Roundstone, Galway,
Collected by Mr. B. Sturges Dodd.
Side and basal views of shell showing the internal folds or plaits, especially characterizing the youthful post-embryonal stage of growth.

In *Clausilia* the mouth is furnished with a number of very characteristic plaits or folds, which vary little in their relative position, and are therefore of specific and taxonomic importance, and extensively relied upon by systematists as a basis upon which to form subgeneric divisions. A full, complete and precise nomenclature, and an accurate determination of the relative positions of the various plaits and folds was thus very desirable, and Messrs. E. A. Smith and B. B. Woodward, with the help of Dr. O. Boettger, have proposed a terminology which is probably the most thorough and satisfactory yet published. These authors recommend the restriction of the term PLICÆ to the plaits situated upon the palatal or outer wall of the shell, and LAMELLÆ to those upon the columella and the columellar-wall above. One of the chief plaits is the plica lunata or lunella, a conspicuous and somewhat arcuate calcareous thickening upon the palatal wall, which is often visible through the shell, but is however somewhat inconstant in form, being sometimes replaced by, or separated into, a series of very short plicæ, ranging one above another in such a way as to suggest the strong probability

that this plait has arisen by their coalescence: in the same way the lamella-fulcrans, which is placed upon the base of the penultimate whorl, would seem to be a result of the thickening of part of the lamella-spiralis, which blends with the similarly thickened lamella-inserta, till they spread across to neighbouring folds, for when the lamella-fulcrans is present, the lamella-spiralis and lamella-inserta are quite absent or so greatly reduced as to be scarcely perceptible. The superior lamella is sometimes joined to the lamella-spiralis, which latter, with the subcolumellar lamella, arises from near the point of attachment of the clausium to the columella.

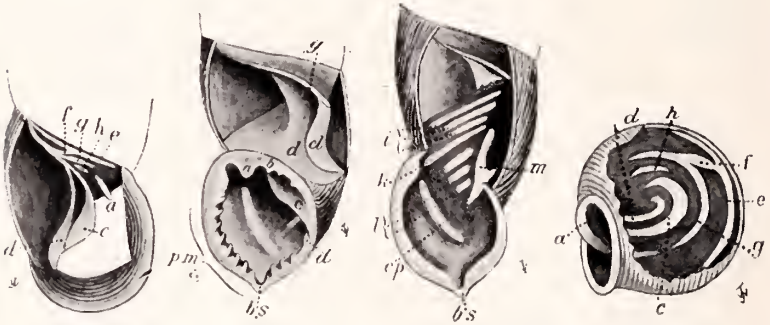


Fig. 147. Fig. 148. Fig. 149. Fig. 150.

Ideal diagrammatic sections of the shell of *Clausilia* to show the position and arrangement of the principal lamellæ and plications characteristic of the genus (modified, after Smith and Woodward).

Fig. 147.—Dorsal view, with outer shell-wall removed to show the lamellæ.

Fig. 148.—Front view with portion of the shell-wall removed to show the position occupied by the clausium and the sub-columellar lamella, and also showing the folds visible exteriorly.

Fig. 149.—Front view with portion of shell-wall and columella removed to show the plicæ.

Fig. 150.—Basal view with shell-wall removed to show the lamellæ.

a. Lamella superior.
b. Lamellæ interlamellares.
c. Lamella inferior.
d. Lamella subcolumellaris.
e. Lamella parallela.
f. Lamella fulcrans.
g. Lamella spiralis.
h. Lamella inserta.
i. Plicæ suturales.
k. Plica principalis.
l. Plicæ palatales.
m. Plica lunata or Lunella.
b.s. Basal or anterior sinus. *cl*. Clausium. *c.p*. Callus palatalis. *p.m*. Plicæ marginales.

The formation of these apertural lamellæ or plications which wind into the shell are considered by Mr. W. H. Dall to be owing to the gradual contraction or narrowing of the later whorls, which necessarily throws into folds or wrinkles the comparatively voluminous mantle margin by compressing it between the muscular foot and the shell-wall. These plications and lamellæ are formed by the semi-fluid secretion from the general surface of the mantle, and are moulded between the folds or wrinkles into which the mantle is thrown, the elevated wrinklings of the mantle pressing against the shell-wall

and allowing only the merest film of shell matter to be deposited there, as they fit into and form the interstices between the apertural ridges moulded by the spaces of the mantle folds. Those species with the retractor muscle affixed high up the spire and which therefore withdraw far within the shell, form the strongest apertural plaits with the greatest prolongations into the interior of the shell.

The normal thickening of the shell towards the aperture, which in some species culminates in the form of a raised internal ridge or rib parallel to and within the outer or palatal margin of the shell, is doubtless a response to the necessity for increased strength at that part in the mature animal. In the immature stages of a mollusk, analogous transverse thickenings may occasionally occur at regular or irregular intervals during growth, and some species, as *Limnæa glabra* and *Limnæa stagnalis* amongst aquatic and *Helix arbustorum* and *Helix nemoralis* amongst terrestrial species, are especially addicted to this habit, which is assumed to be an outward indication of growth checks sustained by the animal, owing to some temporarily unfavourable conditions of the environment.

FIG. 151.—*Limnæa stagnalis* var. *variegata* Haray,
Peffer Burn, Haddingtonshire,
Coll. by Rev. Dr. McMurtrie, F.R.S.E.,
Showing in a fluviatile and in a terrestrial species the transverse thickenings, marking rest periods and indicating the growth checks sustained by the animal.

FIG. 152.—*Helix nemoralis* L.,
Bitton, near Bath,
Collected by Miss F. M. Hele,

FIG. 153. — *Limnæa peregra* var. *marginata* Michaud × 1½,
A pond, Lewes, Sussex,
Collected by Mr. C. H. Morris,
Showing the internal sub-marginal rib, indicative of exposure to drought or of a plethora of calcic matter.

In some of the aquatic species, like *Planorbis spirorbis*, the inhibition of growth owing to exposure to drought is also stated to determine the formation of this abnormal rib or thickening near the apertural margin, this peculiarity being shared by some of the *Limnææ*; a plenitude of calcareous matter will naturally facilitate the formation of this sub-marginal internal rib, which is usually whitish or yellowish in tint, but in *Limnæa palustris* and *Limnæa stagnalis* frequently assumes a deep purple or violet colour.

In some of the *Helices*, as *Helix hortensis* and many other species, the regularly formed internal rib, which forms so conspicuous a feature of the oral aperture in the adult, is developed, according to Longe and Mer, only at the maturity of the shell, owing to the atrophy of certain glands of the margin of the collar, which occupy a furrow or groove parallel with the margin and within which the projecting rib is moulded.

Fig. 154. — *Helix hortensis* Müller (slightly enlarged),
Fordingbridge, Hants.,
Collected by Mr. H. Richardson, M.A.,
Showing the internal sub-marginal rib indicative of maturity.

The Sculpture in Univalves and Bivalves is most usually transverse or parallel with the lines of growth and the margin of the aperture. It is at times very strongly developed and has perhaps its most remarkable example in *Helix aculeata*, where the lamellæ are produced into a beautiful coronet of spines, a form of ornamentation which is unique among British species, but is more numerous amongst tropical genera. The incremental transverse striæ are sometimes conspicuously developed in forms that are generally smooth or have scarcely discernible growth lines, and occasionally specimens are met with in which there is an apparent rhythm in the alternate series of fine and coarse incremental lines, suggestive of positive transverse sculpture, which may be supposed to be due to the more vigorous growth at one time than another. This variation in the prominence of the growth lines is sometimes very regular in its recurrence and produces the ribbed appearance seen in *Helix pulchella* var. *costata*, *Helix arbustorum* var. *rudis*, etc. Reeve has stated that those mollusks developing superficial sculpture are invariably smaller than individuals of the same species in which any kind of decorative sculpture is avoided. This observed fact will account for the disparity in size of *Planorbis nautileus* and its variety *crista*, a characteristic so constant as to have led to the variety being con-

Fig. 155.—*H. aculeata* Müll. ×8,
Bassenthwaite, Cumberland,
Collected by Capt. W. J. Farrer,
Showing the corona of spines.

Fig. 156.—*Helix arbustorum* var. *rudis* Muhlf. (slightly enlarged),
Craig Farm, Montrose,
Collected by Mr. Wm. Duncan,
Showing the regular development of riblets on an ordinarily somewhat smooth shell.

sidered a young stage of the typical form; it is probably, however, like *Helix pulchella*, one of our few dimorphic species. In *Hyalinia radiatula* the sculpture is transversely incised, appearing to radiate from the apex to the periphery, like the spokes of a wheel.

When this incremental sculpture is distinctly developed at somewhat regular intervals into more or less distant costulate ridges, and the spiral sculpture is also elevated and widely separated, the intersection of the elevated spiral and transverse lines causes a sunken or flattened area to be perceptible, forming the sculpture known as decussate or malleate (so called on account of presenting the appearance of being caused by light blows of a hammer or other instrument). These malleations or facets are very often quite regular in their arrangement and necessarily dependent on the direction of the elevated striation to which they are owing. The variety *lacunosa* of *Limnæa palustris* is a characteristic example.

Fig. 157. — *Limnæa palustris* var. *lacunosa* Taylor,
Stream, Leventhorpe Pastures, Leeds,
Showing a regularly decussate or malleate surface.

Fig. 158.—*Limnæa peregra* Müll. × 1½,
Maidenhead, Berks.,
Collected by Mr. C. G. Barrett,
Showing the corrugately malleated surface.

Macgillivray ascribes the rough and corrugately malleate sculpture to exposure to drought, stating that under such circumstances the shell becomes wrinkled and "marked with long ridges or irregular sinkings like the skull of a New Hollander."

The shells of the *Limnæinæ* inhabiting tropical and sub-tropical countries are said to be usually much more constant and uniform in sculpture, as well as in size and shape, than their congeners from more northern districts, and their texture is also finer and smoother on the whole than that of species living in the colder regions.

Spiral or revolving sculpture is rare in British shells, *Cyclostoma elegans* being almost the only species which clearly and strongly exhibits it,

Fig. 159.—External surface of body whorl of *Cyclostoma elegans* Müll., showing the strong spiral ribs and less prominent transverse striation (highly magnified).

though in many other species the spiral sculpture or striation is existent, but not often distinctly perceptible to the naked eye.

The spiral, like the transverse, striation is sometimes incised and not elevated, a character which is naturally not so noticeable and prominent as the elevated sculpture, but is clearly and distinctly visible with a lens upon the surface of many species, offering in *Helix pisana* one of the many characters distinguishing it from *Helix virgata*.

In the Pelecypods the greater or lesser intensity and development of the concentric striæ, which are the representatives of the transverse lines of accretion in the Univalves, are, broadly speaking, the only modification the sculpture undergoes.

The youthful stages of shell growth have also their special characteristics, both in Gastropods and Bivalves; the nuclear or apical whorls in Gastropods always increasing more rapidly in size and being often sculptured or adorned in a different manner to the later growth, have been mistaken for and even described as different species from the parent. *Helix aculeata* has spirally sculptured embryonal whorls, *Pupa cylindracea* an irregularly reticulate pattern thereon, and other species possess more or less distinctive and special characters. The umbones of some Bivalves also exhibit analogous peculiarities, those of *Unio tumidus* having a complex arrangement of nodules and nodular ridges (see p. 42, fig. 102), those of *Unio pictorum* two rows of radiately divergent tubercles on each valve (see page 63, fig. 136), and *Anodonta* a concentric series of prominent angulated ridges and obscure nodulations; these peculiarities being owing to the permanent shell developing within the primitive or glochidian shell of the embryo, the teeth of which prevent the symmetrical and regular growth which characterizes the species

Fig. 160.—*Pupa cylindracea* Da Costa × 30, Isle of Lismore, Main Argyll, Collected by Mr. R. Standen, Showing the delicate reticulate sculpture distinguishing the embryonal shell.

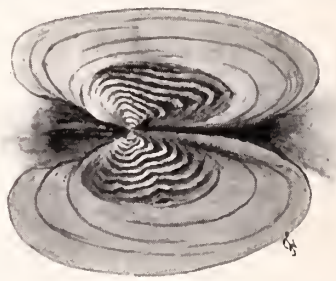


Fig. 161.—*Anodonta anatina* var. *complanata* Rossm. × 8, Gumfrieston, near Tenby, Collected by Mr. F. Walker, Showing the umbonal sculpture characteristic of the species.

when the interference of the larval shell is removed. Other species also possess peculiarities of a more or less striking and distinctive character; but all these youthful characteristics cease to be produced after the youthful stage of growth is passed. There are likewise developed in the youthful stage of *Pisidium henslowanum* peculiar eave-like or wing-like projections, which are naturally formed at the margins of the valves in the young shell, but as growth proceeds the position they occupy is relatively and gradually altered thereby until at maturity they are found at the umbones (see page 42, figs. 103, 104).

As previously remarked, spiral peculiarities in the Univalves, and radiate ones in the Bivalves, arise from the effect of the continued action during growth of those parts of the mantle forming the sculpture, which is in fact moulded upon its surface; the transverse or isolated sculpture being the outcome or result of seasonal or periodic action of the secretory glands.

Abrasion has been held to sufficiently account for the smoothness of shells usually distinctly sculptured, and although friction may account for the smooth and polished state in marine shells, it is not always the true explanation. Specimens or colonies of *Clausilia bidentata* are sometimes met with quite smooth, and this smoothness is evidently not invariably caused by attrition as suggested by Dr. Jeffreys, but is owing to arrested development, the sculpture in them having never existed, or at any rate not proceeded to completion, and indicating non-possession and not loss. This partial exercise of qualities is seen in many other ways amongst mollusks.

Fig. 162.—*Clausilia bidentata* var. *parvula* Turton × 2, Birmingham, Collected by Mr. J. Hopkins, Showing the smooth surface of the whorls arising from the arrested development of the regular sculpture.

Fig. 163.—*C. bidentata* var. *septentrionalis* A. Schmidt × 2, Gairloch, Ross-shire, Collected by Mr. A. Somerville, B.Sc., F.L.S., Showing the usual sculpturing of the whorls characteristic of the species.

Hairy processes of the periostraca, which may be differentiated from spinous processes by being destitute of any interior calcareous support or base and therefore entirely composed of chitinous matter, are a characteristic of many species living in moist shady places and hiding during the day beneath stones, under decaying

leaves or logs, etc.; the mollusks frequenting such situations usually possess shells of a dull and horny tint, without the brightly-coloured markings distinguishing species living a more exposed and prominent life. The epidermis is also more than ordinarily thick and perceptible, and is in some species produced or continued into delicate hairs or bristles, the depressed or flat spired species often possessing hairs of comparatively greater length than those species whose whorls are more conically coiled. The hairs are usually distributed over the surface of the shell in a more or less regular and symmetrical manner, and being developed by processes of the mantle margin and not produced at random, they often have a perceptibly definite arrangement in the different species.

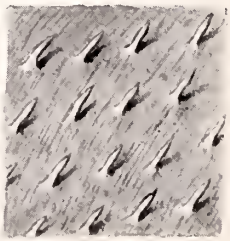


Fig. 164.—Periostracum of *Helix revelata* Mich. showing the arrangement of the hairs upon its surface (highly magnified).

Fig. 165.—A portion of one of the spiral ridges of the periostracum of *Planorbis albus* var. *draparnaudi* (Shepp.) showing the hairs and their arrangement upon the ridge (after a highly magnified original drawing by Mr. G. Sherriff Tye).

According to Mr. W. Jeffery, these hairy processes are formed as thick mucus on the surface of the mantle parallel with the plane of the whorls and are afterwards elevated to their perpendicular position by the succeeding calcareous layers.

Tye has observed that these hairy appendages in the terrestrial snails are hygrostatic in character, and become erect and conspicuous during damp or moist weather, such as these mollusks are most active in, the hairs then forming a *chevaux-de-frise*, probably very repellant to most creatures disposed to prey upon these mollusks, and thus may well be protective. The protective character of these periostracal or epidermal appendages is supported by the fact that many of our larger freshwater as well as terrestrial species, like the *Viviparæ*, *Planorbis corneus*, *Helix cantiana*, etc., are in their young and more helpless stage quite hispid, and thus reap such protection as this defence may afford. The hispid surface of the young *Planorbis corneus* is composed of twenty-five to thirty spiral rows of short

Fig. 166.—*Planorbis corneus* (L.) 15 days old, × 12,
Showing the spiral rows of periostracal hairs characteristic of the youthful stage,
(After an original drawing by Mr. G. Sherriff Tye).

delicate hairs encircling the whorls. In this state the shell is considered to be the *Planorbis similis* of Müller. The *Vivipara contecta* in its embryonal and youthful stage of growth has three principal rows of spirally disposed and comparatively long hairs, of which the two upper rows are the most strongly developed. In addition to these there are from twenty to forty intermediate spiral ridges bearing much more minute and delicate hairs, which rows are always most numerous between the base and the lowermost row of the stronger hairs, and least numerous between the second and the third rows. The number also appears to increase with age, as the penultimate whorl on one specimen which was carefully examined had only five of these finely hispid ridges between the suture and the first row of stronger hairs, while upon the body whorl near the aperture they had increased to twelve.

Fig. 167. — Periostracal hairs or processes upon embryonal *Vivipara contecta* Millet (highly magnified), Manchester, (After an original drawing by Mr. G. Sherriff Tye).

The development of hairs is very variable amongst individuals of the same species; thus the v. *hispidosa* of *H. hispida* is a very good example of hypertrichosis, being densely covered with stiff recurved white hairs, while Alder's v. *depilata* of the same species is almost bald; possibly these differences are a more or less direct result of the environment of the two forms.

Fig. 168. — Periostracal hairs of *Helix revelata* Michaud (highly magnified), Plymouth, Devon. (After an original drawing by Mr. G. Sherriff Tye).

Fig. 169. — Periostracal hairs of *Helix granulata* Alder. (highly magnified), Halifax, Yorks. (After an original drawing by Mr. G. Sherriff Tye).

These hairs are generally caducous, cylindrically subulate and often borne upon a little tubercle or swollen base, and are more especially a characteristic of thin and dull coloured species, varying in their character according to the species; those of *Helix revelata* being somewhat short and thick, and those of *Helix granulata* much longer and more slender, with knotty prominences at irregular intervals,

while those of *Helix hispida* are usually more or less angulated or bent, with the tips directed forwards or towards the aperture of the shell.

These periostracal hairs are not confined to the Gastropods, but are equally possessed by the different species of *Pisidium*, *Sphærium*, etc.; those upon the shell of *Sphærium corneum* are of microscopic size, somewhat short, comparatively thick, bent at the tips and most numerous in the umbonal region.

Substance, or thickness, is frequently the outcome of an ample or a limited supply of calcareous matter, though the variation in this character may also arise from an apparent physiological inability to utilize the material presented, which action may be intensified or diminished by chemical, meteorological, or other conditions. This weight or thickness varies not only according to the species, some having thin and almost purely chitinous shells while others are heavy and dense and almost entirely composed of calcareous matter, but also according to age, young specimens being always more delicate than adults living under the same conditions and containing proportionately less calcic carbonate than the more aged shells, in which the nacreous or inner layer may become abnormally thickened if the life of the individual be from any cause greatly prolonged.

It has also been satisfactorily and conclusively shown that a temperature above or below the optimum, which optimum varies for the different species, results in the minimising or even the cessation of the shell-secreting function, and the growth, if any, is characterized by greater delicacy as the temperature recedes from the optimum. Thus the varieties *glacialis* and *thermalis* of *Limnæa peregra* which inhabits glacial and thermal springs respectively, are equally distinguished for the extreme delicacy and dwarf size of their shells. Specimens of *Limnæa peregra* found living in the warm water of engine cisterns at Cheadle, Burnley, and other places, are characterized by the same extreme tenuity and diminished size. This form is almost equally well-known by the two distinct names, *diaphana* and *thermalis*, the first descriptive of the character of the shell and the second referring to its habitat.

Fig. 170.—*Limnæa peregra* var. *thermalis* Boubée × 1½,
Mill cistern, Gannow, Burnley,
Collected by Mr. R. Wigglesworth,
Showing the effect upon the shell of too great a degree of warmth in the inhabited water.

The Burnley shells are, as I am informed by Mr. F. C. Long, subjected to a temperature of 84° Fahr., and are especially transparent

and also of diminished size; the Cheadle specimens of the same species, though smaller and thinner, are less transparent than the Burnley shells, and are, according to the careful and connected observations obligingly undertaken at my request by Mr. Masefield, subjected to a temperature varying between 60° and 98° Fahr.; when the water rises towards the latter temperature these mollusks crawl out from it and remain attached to the sides of the condensing reservoir at some point above the water level until evening, when the temperature owing to the stoppage of the engines, begins to fall again, and on its decreasing to about 98° the mollusks have been observed to re-enter the water, that temperature appearing to be the maximum heat they are able or willing to endure.

Fluviatile species inhabiting great depths, much beyond those in which they are normally found, also show marked attenuation of shell substance, probably on account of the lower temperature to which they are exposed hindering the free exercise of the shell-secreting function. The *Limnæa stagnalis* dredged by Mr. Bryant Walker in High Island Harbour, Lake Michigan, at a depth of 34 feet, is remarkable for the delicacy of its shell, and this is also a very striking character of the various abyssal forms of *Limnæa* from the depths of the Lake of Geneva.

In *Helix aspersa* v. *tennior* found in Guernsey, where calcareous strata are absent and the shell more largely composed of animal matter, we have a very good example of the effect of a deficiency of shell-forming material, the weight of a fairly characteristic specimen of this variety, kindly given me by Rev. Dr. McMurtrie, being only four grains, whereas the average weight of typical shells is about 32 grains. *Helix nemoralis* shows similar, though less striking, results, as specimens found by Mr. J. Ray Hardy upon the Volcanic Slate, near the summit of the Macgillicuddy Reeks, co. Kerry, were so excessively thin that many of the most fragile collapsed under the necessary compression used in gathering or cleaning them, the most delicate shell preserved intact weighing 3·3 grains, or a little more than one-quarter of the weight of ordinary individuals.

This deficiency of calcareous matter has also, according to Clessin, often a marked effect upon the form of certain species, the shells of *Clausilia* being said to diminish in length and *Helix lapicida* to become rounded at the periphery.

The opposite or incrassate condition may be well illustrated by *Helix aspersa* var. *solidissima* Paulucci, a specimen of which, found by the late Mr. C. Ashford on the Purbeck limestone at Swanage, though of only normal size, weighed eighty-three grains; and Mr. C. Jefferys has taken several specimens on the cliffs at Tenby weighing over one hundred grains each, or more than three times the weight of average individuals.

Helix nemoralis normally weighs about 11 grains, yet a thick shelled race, the variety *creticola* of Mörch, which formerly existed in the West of Ireland, and in a somewhat less pronounced form has been shown by Mr. Collier to still exist there, attained a much greater weight. A number of sub-fossil specimens of this variety, kindly sent me by Prof. D'Arcy Thompson, had an average weight of 44 grains, the heaviest weighing 79 grains and the lightest, a somewhat diminutive shell, weighing 15 grains. This abnormal incrassation of the shell substance is principally caused by the secretion of additional and thicker layers to the inner surface of the shell, and probably arises from the mollusk living upon suitable geological strata, furnishing abundant supplies of calcic matter, and also from the probable prolongation of the life of the animal beyond the usual life-limit of the species, perhaps owing to a succession of mild and equable seasons, the periodical deposition of the shell matter by the visceral mantle occurring regularly at its proper season during the whole life of the animal. Post-mortem deposits of calcic carbonate, by carbonate of lime entering the pores in a fluid state, have been suggested as the cause of the unusual thickness of these shells, but a careful examination of sections through the shell disprove this suggestion, as they clearly demonstrate that this extreme incrassation of the shell has taken place in a strictly normal manner, the inner layer upon the base of the preceding whorls retaining its characteristic comparative tenuity, being only modified by the delicate films of calcic matter, deposited at the same time as the stronger layers which thicken the interior

Fig. 171. — Section through the shell of a normal *H. nemoralis* L., showing the usual thickness and other characters of the species. Weight of section, 8 grains.
From a section cut by Mr. F. Rhodes.

Fig. 172. — Section through the shell of a sub-fossil *H. nemoralis* L., from Dog's Bay, Connemara, exhibiting the remarkable thickening of the shell-wall. Weight of section, 43 grains.
From a section cut by Mr. J. Ray Hardy.

surface of what is or were the external shell-walls, and therefore preserving the same relative thicknesses of the external and internal shell-walls that distinguishes normal specimens.

Fluviatile species, though affected by the comparative abundance or scarcity of calcic matter in relation to the thickness attained by the shell, are also influenced greatly by other circumstances of their environment, those individuals inhabiting rough or disturbed waters, rapid and turbulent streams, etc., develop a thicker and stronger shell than usual to better enable them to withstand the force of the waves and currents to which they are exposed, and often show a shorter spire and a more expanded and larger mouth, which necessarily allows for greater clinging or adhesive power, and renders the mollusk less liable to be detached and probably injured by wave violence.

In Anodons the light inflated form with thinly calcified valves may, as in the Univalves, exhibit according to circumstances an actual scarcity of shell-forming material or a physiological inability to utilize it. Shallow waters with their greater variations of temperature and consequent checks to shell secretion, tend to produce thin and lightly calcified shells, as do also the immense depths known to exist in some lakes, perhaps in this case due to the constant low temperature, much below the optimum for the species.

The effect of a plethora of calcareous matter or of functional activity of the secretory organs is strongly exhibited in *Anodonta cygnea* v. *incrassata*, and is shown not only by the greatly thickened nacreous layer, but the plenitude of calcareous substance is often strongly indicated by a heavy deposit of the limy matter in the form of tufa, on the exposed posterior end of the shell.

A characteristic specimen of this variety from a brook at Tisbury, Wiltshire, kindly given me by the late Mr. J. Pickering, weighs 2,227 grains or 5·12 ounces, while an example of the typical form of equivalent size from Nagden, near Faversham, collected by the late Miss E. B. Fairbrass, weighed only 322 grains, or about one-seventh the weight of the variety *incrassata*. Rough and deep waters, although not profound depths, are both said to tend to produce thicker and stronger shells than those developed in shallow and more tranquil waters.

Some species, as *Unio margaritifer* and *Neritina fluviatilis*, appear able to extract the necessary lime carbonate to form thick and heavy shells even from the waters of granitic districts, whilst

other species, as *Ancylus fluviatilis*, under similar conditions seem unable to do so, their shells being unusually delicate and thin.

This difference in the selective working of the tissues in different species is true also in a lesser degree amongst the individuals composing a species, which vary *inter se* in their power to utilize the shell-forming material presented, although the thickness of the shell would generally seem to be in inverse ratio to the hardiness of the animal, the most hardy species or genera, or those which withstand the most rigorous climates having only a thin external or internal shell, as though the shell-forming energy of the creature was diverted to strengthen more vital processes.

Size is not only influenced by the obvious causes of the abundance or scarcity of suitable and nutritious food, the result of which would be the production of a larger or a more diminutive animal and shell than would be developed under ordinary conditions, but is also in a large degree dependent upon temperature and other circumstances. The researches of Semper on the phenomena of growth, upon which size is dependent, have shown that in *Limnæa stagnalis* the size attained by the shell is capable of correlation with the temperature and amount of the inhabited water, as assimilation and growth equally ceased if the degree of warmth exceeded 90° F. or fell below 53° F., the fullest vigour being enjoyed and the largest size attained when the temperature ranged between 68° F. and 77° F.

The results of these researches are of great interest, and are more or less applicable to other species, as demonstrating some of the conditions governing growth—and therefore size—in mollusca generally, and clearly establish that the volume or amount of water allowed to each mollusk is so decisive in its effect upon growth that in the space of six days the difference in the size of the shells of those in a large and those in a small body of water becomes apparent ; the smaller the amount of water per individual the smaller the shell and *vice versâ*. If the volume of water be less than 5,000 cubic centimetres per individual, a dwarfing influence is perceptible, the greatest differential effect being

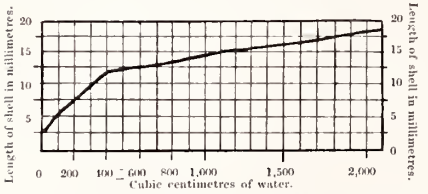


Fig. 173.—Volume-curve of *Limnæa stagnalis*, showing the effects of various volumes of water upon the size attained in a definite period of 65 days (after Semper).

shown between those shells inhabiting 100 and 500 cubic centimetres respectively; for, whereas specimens reared in 100 cubic centimetres of water only acquired a length of 6 mill. in 65 days, those in 250 centimetres reached 9 mill., those in 500 centimetres 12 mill., while the individuals in 2000 cubic centimetres grew to 18 mill. in the same space of time. Ample food and healthy conditions had been assured to each mollusk, and the experiment therefore exhibits the dwarfing effect of too great an abundance of life in any circumscribed area apart from scarcity of food. The rate of growth

FIGS. 174, 175, 176, 177.

Four shells of *Limnæa stagnalis*, each 65 days old and hatched from the same mass of ova, but reared in different volumes of water to demonstrate the effect of the amount of water per individual upon the size attained in a definite period of time, and illustrating the Volume-curve Fig. 173.

Fig. 174, reared in 100 cubic centimetres of water; Fig. 175, in 250; Fig. 176, in 500; and Fig. 177, in 2,000 (after Semper).

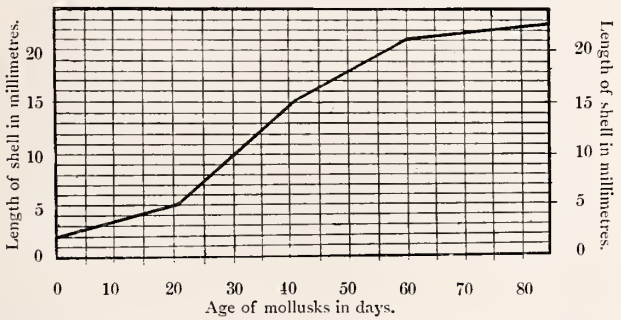


FIG. 178.—Curve of time, showing the average rate of growth of *Limnæa stagnalis* reared in from 1,000 to 2,000 cubic centimetres of water (after Semper, modified).

is also far from uniform, as at first the young *Limnæa* grows at a moderate rate, after which follows a period of quickened growth, until

FIGS. 179, 180, 181, 182.

Four figures of the shell of *Limnæa stagnalis* to show the amount and rate of increase in size and to more strikingly demonstrate the period of most rapid growth, averaged from specimens reared in from 1,000 to 2,000 cubic centimetres of water, and illustrating the Growth and Time-Curve, Fig. 178.

Fig. 179, 21 days old; Fig. 180, 42 days old; Fig. 181, 60 days old; and Fig. 182, 85 days old.

at length, the older the animal the slower the growth. Maximum size can only be attained by favourable conditions at these early and critical periods, especially that of greatest increase, as that period once passed cannot afterwards be fully compensated for by any subsequently favourable conditions, the shell being then constructed on a more

diminutive scale. A specimen that does not exceed 20 mill. in length during the first season is necessarily undersized when adult.

Temperature exercises a very powerful influence upon the size attained, as the young *Limnæa* only begins to assimilate food and therefore grow, when the water attains a temperature of about 53° Fahr., and although a much lower temperature does not seem to be vitally injurious to the mollusk, its effects are exhibited in the decreased power of assimilation and consequent checks to, or inhibition of growth.

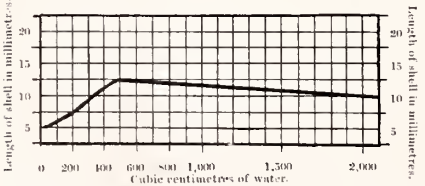


Fig. 183. — Volume-curve of *Limnæa stagnalis*, totally altered by a sudden fall of temperature arresting the growth. The various vessels containing the unequal bodies of water in which the *Limnæa* lived, stood by a window where the sun shone for about two hours in the afternoon, elevating the water in the smaller vessels to a favourable temperature, but being insufficient to do so with the larger ones. Hence the *Limnæa* in the largest vessel containing 2,000 cubic centimetres of water, which should have been under ordinarily favourable circumstances very much larger, were actually smaller than those in many of the smaller vessels (after Semper).

Semper has experimentally demonstrated the effect of cold in retarding the growth of specimens in every other respect quite as favourably circumstanced as those attaining a much larger size.

The mean temperature of a district may be apparently favourable to a species, but this average may be the result of two extremes, and these extremes of temperature, if occurring during the growth period have a baneful influence and unfavourably affect the size attained by the animal.

Figs. 184, 185, 186, 187.

Four figures of the shell of *L. stagnalis* showing the reduced size attained owing to the temperature of the inhabited water becoming lowered to nearly 55 Fahr., and illustrating the Volume and Growth Curve, Fig. 183.

Fig. 184, reared in 100 cubic centimetres of water; Fig. 185, in 250; Fig. 186, in 500; and Fig. 187, in 2,000 (compare Figs. 177 & 187).

During the winter months, however, most of our land and freshwater mollusks are more or less complete hibernants, but on the termination of this winter dormancy there quickly follows in the young a period of rapid assimilation and growth, and unfavourable influences at this season necessarily retard the growth and induce dwarfed shells, as no after favourable circumstances can fully compensate for retardation of growth in early life.

Thus we are enabled to understand and appreciate the periodic variations in size and the characters in correlation with it, so often noticed to occur, more especially amongst the freshwater mollusks, and to consider them with great probability to be the biological

expression of the various climatic and other modifying circumstances to which the mollusks have been subjected. A cold unfavourable season would result in a smaller and more delicate shell, with probably more or less distinct transverse indications of the growth-checks sustained, while another season of a milder and more favourable character would result in larger and more uniformly grown specimens.

In Malham Tarn, a large body of water upon an elevated plateau, 1,250 feet above the sea, in the West Yorkshire Highlands, Mr. W. Denison Roebuck and Mr. J. Darker Butterell, in Sept., 1883, collected numerous specimens of *Limnæa stagnalis*, which I found to clearly reflect the low temperature and the thermometric vicissitudes of the lake by a shell of great comparative delicacy and small size, with the many growth-checks strongly emphasized by the whitish transverse thickenings crossing the whorls and showing that part of the shell-forming energy has evidently been here diverted to more vital purposes. Other specimens obtained during August, 1890, from the same place, did not exhibit any striking diversity from ordinary examples, and this was probably owing to the active growth-periods being during comparatively mild and favourable weather.

FIG. 188.—*Limnæa stagnalis* var. *fragilis-variegata* Roeb., Malham Tarn, Yorks., Sept., 1883, Collected by Mr. W. D. Roebuck, Showing its maturity by the full number of whorls and the inclement nature of the growth periods by a small thin shell, with many strong indications of growth checks.

FIG. 189.—*L. stagnalis* (L.), Malham Tarn, Yorks., Aug. 1890, Collected by Mr. W. D. Roebuck, Showing the even regular growth and larger size, as attained under more favourable circumstances.

An examination of the meteorological statistics preserved by the Philosophical Society at Leeds confirm and emphasize the probable correctness of my conclusions. The early spring of 1883 was characterized by severe cold, frequent snow storms, and considerable fluctuations of temperature, while that of 1890 was distinctly more equable, and showed fewer and slighter variations of temperature.

For every other species there are probably also certain conditions of temperature, etc., exceptionally favourable to their growth and development, which may be termed the optimum, subject to which conditions progress and growth are most rapid and decisive, being

either more vigorous while in progress, or the growth season longer continued, the result in each case being the development of a larger animal and shell. As this optimum environment probably varies for each species, it follows that where these optimum conditions are most nearly approached, the species most favourably affected will develop the largest and most vigorous mollusks, and divergence from this optimum would result in a proportionately smaller animal and shell.

Equability and suitability of temperature during the growth period, which is essential to the development of the finest mollusks, is not exclusively dependent upon latitude, being largely influenced by the configuration of the land, the vicinity of the sea, and the prevailing direction of winds and currents. Thus the British Isles, and more especially Ireland, have—owing to their insular position and other causes—an equable and moist climate, and do not suffer from the great heat in summer and the intense cold in winter that characterize the great continental areas in the same latitude, each of which imposes a check upon growth if occurring during the growth season.

Fig. 190.—*Helix aspersa* var. *major* Pascal,
Algiers, N. Africa,
Showing the effect of a favourable environment.

Dr. Jeffreys has asserted that northern specimens generally attain a larger size than the same species in the south, and quotes Draparnaud's remarks on the comparative size of the shells of north and south France in support of his opinion; but this result can only occur with such species as are most suitably circumstanced in such districts, and this is not merely a question of a larger food supply being obtainable, owing to the greater paucity of species and individuals in northern districts, as Dr. Jeffreys has supposed, but is dependent, amongst other things, upon the existence of a temperature at which assimilation can be actively carried on.

Fig. 191.—*Helix aspersa* var. *minor* Picard,
Cardiff,
Collected by Mr. F. W. Wotton,
Showing the effects of some unfavourable conditions of the environment.

Specimens of *Helix aspersa* from our own country are far inferior in size to

the gigantic examples of the same species found in Algeria, and our average *Planorbis corneus* are quite diminutive compared with specimens of the same species from southern Europe.

Inversely *Balea perversa* would appear to find in North Britain and in elevated situations its most congenial habitats, the Scottish specimens being perhaps finer examples of the species than those from more southern and warmer localities.

Granitic soils, peaty districts, or any formation deficient of the calcic carbonate of which shells are mainly composed, are characterized by shells not only of thin texture but dwarf size; this diminution of size is also an effect of altitude, crowding of individuals, and, according to M. Locard, of darkness, or indeed of any other environment unfavourable to the fullest development of the species; the vicinity of the sea would also appear to have a dwarfing influence upon terrestrial and fluviatile mollusks unless counter-balanced by other exceptionally favourable circumstances, and the same effect is produced by very deep waters, such localities also exercising a dwarfing effect upon the species inhabiting them.

A diminutive size in freshwater shells may also be a result of too great an abundance or overcrowding of individuals in the area occupied, as demonstrated by Semper, who has enunciated as a general principle that large bodies of water develop large shells, and ponds or other bodies of water much restricted in area produce small shells; and this is asserted to be a general rule with fishes also, it being well known that the further one advances up-stream and the smaller the Trout become.

The Colouring of the mollusca seems largely dependent upon the action of light, the more exposed surface of spiral shells and the posterior end of burrowing Bivalves being usually more richly coloured or ornamented than the less exposed or buried portions, and colouring generally is probably of great biological importance; it is also, as in other groups, most pronounced in brilliancy and variety in the warmer regions of the globe, and becomes gradually reduced in diversity and beauty as the poles are approached. These known facts led Dr. Fischer to propose for the mollusca three zones of colouration corresponding with the thermal ones, viz.:—

Polychromic, for the brilliantly coloured shells chiefly inhabiting tropical countries. Examples: *Liguus virgineus* (L.), West Indies, pl. ii., fig. 8, and *Helix picta* Born, Cuba, pl. ii., fig. 9.

Oligochromic, for the more soberly coloured and less varied shells of the temperate latitudes. Examples : *Helix pisana* Müller, Mentone, pl. ii., fig. 10, and *Helix nemoralis* var. *libellula* (Risso), Bath, pl. ii., fig. 11; and

Monochromic, for the simply coloured species characterizing the colder regions. Examples: *Vitrina pellucida* var. *depressiuscula* Jeffr., Exeter, pl. ii., fig. 12, and *Vertigo alpestris* Alder, Cottingley, pl. ii., fig. 13.

Many exceptions naturally occur to these broad lines of distinction, as these results are naturally more or less influenced and modified by nature of soil, vegetation, altitude, and other circumstances, but there can be no dispute that they express the leading features of colour distribution upon the globe, though species with strong shells are usually more vividly coloured than their congeners possessing fragile and delicate ones.

Colouring in the mollusca may be due to the structural character of the surface of the shell diffracting and dispersing the light rays, but is more generally owing to the absorption of certain of the elements of light by the special substances in the shell termed pigments, the particular colours produced varying according to the chemical nature of the constituents of the shell displaying the colour, and being due to those rays or vibrations of light which are not absorbed, but reflected to the eye ; thus red is the result of the absorption of all but the red rays which are therefore reflected and visible, while black is owing to the absorption of all the constituents of light, and white to their complete reflection.

Structural or iridescent colouring is strikingly exhibited by the inside of the valves of the Naiads, as well as occasionally by the interior surface of some Univalves, and is owing not to the varied absorptive power of certain of the component parts of the shell, but to a multitudinous series of undulating parallel lines of exceeding fineness which diffract the light and give rise to a prismatic play of colour, varying from red, through yellow, green and blue to violet, according as the point of view becomes more and more oblique and the lineation thereby more closely approximated, owing to the varying angles at which the surface is seen.

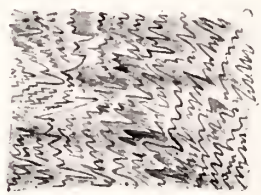


Fig. 192.—Highly magnified surface of a nacreous shell, showing the minute parallel sculpture upon which structural or prismatic colouring is dependent (after Tryon).

That this prismatic colouring is largely due to the light rays impinging on the innumerable finely incised lines is demonstrated by the fact that the iridescent effect has been successfully imitated on steel buttons by engraving upon them similar fine and parallel lines. In some species this beautiful effect is probably to some extent due to the thin laminated structure of the nacreous layer. All nacreous shells, however, when polished become iridescent and form more or less brilliant mother-of-pearl.

The colouration of the body of the animal, speaking generally, would often appear to have little or no relation to that of the shell, for *Helix nemoralis*, which has the most brilliantly and variously coloured shell of any of our native species, has an almost uniformly coloured animal, and uniformly horn-coloured shells are not always borne, as might be expected, upon uniformly coloured animals, but on the contrary are sometimes, as in *Limnæa*, tenanted by animals with the mantle strongly maculated and marbled with black and yellow. The naked forms are also more brilliantly and variously coloured than the animals of the testaceous species.

Shells which live most freely exposed to the light, if other circumstances be favourable, are the most brightly coloured, as *Helix nemoralis* and *Helix hortensis*, which sometimes almost rival tropical species in the brilliancy and variety of their colours and banding, varying from almost pure white, through yellow, pink, and chestnut, to deep chocolate brown, while those species usually found secreted during the day under stones, logs, etc., like the *Hyalinia*, or which habitually live on the ground or the trunks of trees, like the *Bulimini*, approximate to these objects in aspect, their colouring being PROCRYPTIC or protective in character, the exceptions being the white or colourless species, which however are usually of small size and very retiring in habit.

Shells like those of *Limax*, which are developed within as well as concealed by the mantle and thus excluded from light, are always white or colourless, and do not exhibit the diverse and varied tinting acquired by external shells.

In clear bright water the *Anodons* and *Uniones* are often of a bright green colour, sometimes beautifully rayed by a deeper tinge of the same hue or by distinctly yellow or brown shades of colour; according to Herr Jordan the radiate varieties are chiefly but not invariably found in flowing waters; but the shells inhabiting the

more turbid rivers and ponds, or any waters contaminated with sewage, etc., do not normally exhibit this bright and variegated colouring, but are often of various shades of brown verging occasionally upon black.

In our Gastropoda the colouring matter is generally speaking resident in the calcareous part of the shell, and in the Pelecypoda is found in the periostracum or epidermis, but the colouring of some Gastropods, as *Helix aculeata*, *Clausilia laminata*, etc., is entirely or chiefly due to the periostracal investment, and not to the pigmentation of the calcareous part of the shell, such species resembling the Pelecypoda in this respect. According to Krukenberg the red, yellow and brown pigments, which are the most prevalent colours amongst mollusks, belong to the Lipochromoids or Melanoids.

Brown of various shades is the most prevalent colour amongst both our land and freshwater shells, although some freshwater species are of a bright green, a colour not found amongst our land shells, the nearest approach to it being by *Helix revelata*, which in some localities shows a strong though dull greenish shade. Camerano, who has studied the Mollusca generally with the object of determining the relative frequency of the various colours, finds that black is rare, brown, grey, yellow, white and red all common, violet relatively common, while blue and green are more rarely met with.

The pinks and violets are usually the most evanescent colours, and colouring generally amongst our land and freshwater mollusks seems to be more or less fugitive, if abnormal or unusual as to position, thus the delicate purple sometimes found on the lip of *Helix aspersa* soon fades and disappears. The normal dark spiral banding of the fusco-labiate variety of *Helix hortensis* seems practically permanent, but the abnormal colouring of the lip is unstable, the pink element first disappearing, followed more slowly by the brown.

Land shells may be modified or changed in colouring by adventitious matter about their food, as Herr Tischbein has observed in Germany that *Helix hortensis* when found in the neighbourhood of tanneries assumes a peculiar brownish hue. Aquatic shells are also liable to be similarly affected by substances intermixed with or dissolved in the water they inhabit, as Mr. Quilter has recorded that specimens of *Unio pictorum* found in a certain part of Groby Pool, Leicestershire, adjacent to a local out-crop of red triassic marl, had the nacre tinged of a beautiful salmon colour by the oxide of iron

derived therefrom, the shells found in other portions of the pool being quite normal in this respect; and Mr. Heathcote noticed that during the long drought in 1887, when the Ringley Canal was very low and the surface covered by an iridescent scum from the aniline dye-works, that all the *Limnæa stagnalis* in that locality were remarkable for a noticeable metallic gloss and were much darker in colour, and more strongly striated than normally; but the specimens collected in the same place when the canal was high and clear were characterized by the usual delicate pale horn colour and smooth texture of ordinary individuals.

All aquatic shells whether univalve or bivalve are at times and in certain localities entirely or partially covered externally with a reddish tint; this is usually owing to living in ferruginous waters and is caused by an extraneous deposit of oxide of iron. Analogous incrustations of tufa, carbonaceous or other mineral and confervoid matters, give to the exterior of aquatic shells different tints, in accordance with the nature of this superficial investment, and have given rise to some unnecessary varietal names.

The peristome is sometimes identical in colour with the general surface of the shell, but often, especially in those species with thickened or distinctive lip structure, the colour is strikingly different, as in the brown or horn-coloured shells which usually have the peristome pure white, occasionally tinted with a delicate rose colour. In other species, as *Helix nemoralis*, the colour of the lip is very variable and its special tint may overspread not only the umbilical callosity, but the surface of the penultimate whorl, and even extend for some distance into the interior of the shell. This lip colouring, especially if not an ordinary characteristic of the species, is often very fugitive in character and soon fades after the death of the animal. Draparnaud has observed that the peristome of *Helix pisana* may become of a bright rose colour if the animal be kept without food for a length of time, and the same result is said to occur if the animal lives in warm and sunny places, this colouring being said to be deficient in those individuals living in less favoured spots.

Albinism (*albus*, white) is generally owing to pathological causes and is therefore strictly speaking a morbid condition of the animal, consequent upon the impaired secretive power or abortion of the colour glands, and their consequent physiological inability to secrete

the requisite colouring matter, but perhaps in some cases from an actual deficiency of pigment-forming material.

Albinism may be a more or less partial phenomenon, affecting only a certain set or sets of organs, and not modifying others, or may embrace the whole animal, thus the shell of a mollusk may be destitute of colouring or pigmentation and therefore an albino, without the animal itself being necessarily albine. In fact, instances are numberless in which a strongly pigmented animal has borne an albine or colourless shell, and the possibility of this is easily appreciated when it is seen that the albinism of the shell solely depends upon the selective working of the glands of the mantle margin, which are extremely susceptible to different influences, as is shown by the fact that one can hardly take up a specimen of certain of our land shells without noting the variability in the intensity of the colouring of the ground tint at different periods of growth, this being even more strongly exhibited by the spiral banding, which is frequently found to be totally destitute of colouring matter at the commencement of a periodic growth, often acquiring the normal depth of colouring by slow degrees only and as the termination of the growth period is approached.

True albine shells are quite deficient of coloured pigment and may have an opaque or a translucent character depending upon the disposition of the constituent particles forming the shell, as to whether they reflect the light rays or allow their passage through the shell substance, and must not, as is sometimes the case, be confused with bandless specimens of normally banded species which may happen to possess a whitish ground colour, and are therefore merely ordinary individuals in which the banding is suppressed: this difference is well illustrated by the translucent-banded form of *Helix virgata* and the variety *albicans*, the first being true albinos, while the latter are only ordinary individuals in which the banding is deficient (see pl. ii., figs. 4, 5). Parallel cases are furnished by other species, *Helix pisana*, for instance, showing the two forms in the varieties *alba* and *albida* respectively.

The occasionally different colouring of the nucleus of the shells not truly albine is sometimes relied upon as a means to readily distinguish the true albinos, but this test is not an infallible guide. An albine shell, when borne by a pigmented mollusk, is essentially similar to any white-furred or white-feathered animal or bird, as the shell, like fur or feathers, is an essentially cuticular structure quite outside the animal, and, though organically connected, it has been satisfactorily demon-

strated that a *Helix* can exist even when its organic connection with the shell is completely severed.

It is quite certain that local circumstances do at times conduce to the development of albine shells. One instance will suffice to support this view ; under stones in a dell on the cliffs near Hele Bay, Ilfracombe, Mr. Brockton Tomlin, in March, 1887, found hundreds of the white variety of *Helix rotundata*, and it is suggestive that this state was practically universal and not confined to this particular species, but was shared in by the associated species, *Hyalinia cellaria* and *Arion hortensis*. This variation, so plentiful within these narrowly circumscribed limits, was not met with elsewhere in the neighbourhood, clearly showing that the influence, whatever its nature, did not extend beyond the limits of this little valley.

Amongst Lepidoptera Mr. Poulton has satisfactorily shown that the character of the larval food affects its colouring. He especially instances *Triphæna pronuba* fed in darkness upon the midribs of cabbage leaves, which were quite unable to form the green and brown colouration, although others fed under similar conditions upon more normal food were typically coloured. Moquin-Tandon considered one of the principal causes of albinism in mollusks to be the nature of the soil and consequently the food, and as some corroboration of this opinion it may be stated that M. Jules Colbeau long ago observed and recorded that about Dinant the translucently-banded *Helix hortensis* exhibited a noticeable partiality for gooseberry bushes, and Mr. A. E. Boycott has recently remarked upon the predilection of this and other albine forms for plants of the horse-radish, but although these observers did not pursue the investigation further, yet it has been actually demonstrated by Capt. W. J. Farrer that this albine modification may sometimes be of a phytophagic character as a change of diet in connection with the different environment of captivity proved to be sufficient to cause albine growth upon shells previously almost melanic in colouring. A number of half-grown shells of *Helix hortensis* var. *olivacea* and *Helix arbustorum* var. *fusca* were gathered at York and conveyed to Bassenthwaite, in Cumberland, and there fed to maturity in captivity upon the leaves of turnip and cabbage, the new growth in both species was of quite an albine character and the junction of the contrasting colours sharply defined; but Mr. T. Scott has recorded an almost exactly opposite experience, a young *Helix arbustorum* var. *flavescens* fed upon cabbages, turnips,

etc., formed the new growth of a much darker colour than before, although it is possible that in this case the different result may be due to the additional articles of diet not enumerated.

According to M. Malard and other observers concealment by isochromatic adaption to environment is very common amongst crustaceans and other organisms, and we apparently see a striking example of this interesting phenomenon in the albine specimens of *Pupa cylindracea* found by Capt. Farrer upon a whitewashed wall at Bassenthwaite, the white variety being confined exclusively to the whitewashed portion, the type form existing only upon that part of the wall left in its natural condition; as collateral evidence of the probable accuracy of the supposition that we have here a case of this isochromatic adaptation to environment, without, however, defining the process by which this adaptation has been brought about, whether by the elimination of the normal form or other method, I may recall the record given by Semper, on the authority of Dr. Braun, that white rabbits are most certainly and easily reared in a white reflected light.

It is now well-known and acknowledged that albinism is hereditary and may be transmitted to offspring. This is not only practically established by experience of the shells under natural conditions, but has been frequently demonstrated with mollusks kept in captivity.

The increase in numbers of the specimens of a white variety, to the disadvantage of the typical form dwelling with it, points only to the persistence of some features of the environment favourable to the variation or, according to Gredler, indicates that the species has reached the extreme limit of its horizontal or vertical distribution.

There appears to be a somewhat general consensus of opinion, especially amongst Continental conchologists, that albinism in the shell occurs most freely amongst those mollusks inhabiting cold, misty and sunless localities, and the unusual numbers chronicled by them during dull and sunless seasons and from subalpine districts, which have something of this character, supports the theory, as also does the assertion of Herr Dietz that examples of *Helix hortensis* of an albine character are most commonly found in wet years, and that those with banded shells in normal seasons, have the growth of a wet season deficient of the usual pigment.

Diametrically opposed to the preceding theory is the suggestion that dry, warm and sunny seasons are favourable to shells assuming the albine state, and there is some reason from analogy in believing

that such conditions will assist in the elimination of colouring matter, and tend towards the dull white and bandless forms especially characteristic of arid and desert districts.

Leucochroism (λευκός white and χροιά colour) has been defined as that state wherein the darker shades of the ground colouring or the markings thereon are diminished in intensity, in extent, or both combined, owing to the diffusion of a paler shade of colour, or to the darker markings assuming a paler tint than is usual in typical individuals. This state may be considered as more or less intermediate between the ordinary typical condition and the albine form, and the illustrations of this variation are very numerous amongst mollusks, the bandless varieties or the pale or thin banded forms of *Helix nemoralis* and the dull white bandless varieties of *Helix virgata* may be quoted as familiar instances (see pl. ii., fig. 4). One of the causes of this state has been assumed to be exposure to dryness and warmth, circumstances which M. Strobel has shown to induce this state in *Helix virgata*, and the accuracy of this opinion is confirmed by the knowledge that such forms are the prevalent ones in desert regions, their colouring reflecting the heat to which they are exposed, and therefore preventing the drying-up of the natural moisture of the animal. Mr. Dall thinks this leucochroic condition may be due to a less fluent secretion of the animal products, which are the chief components of the glistening epidermis of shells native to moister regions. This and other variations may however also arise as a consequence of the protection afforded by resemblance to their surroundings, as may to a certain extent be the case with the variety *albescens* of *Cyclostoma elegans* found by Mr. Brockton Tomlin, upon the white chalk cliffs at Lulworth.

Melanochroism (μέλᾶν black and χροιά colour) is the opposite tendency to leucochroism, as it expresses the increase of darker shades, either of the ground tint or markings, at the expense of the lighter shades of colour, and is a tendency towards true melanism, being the intermediate stage between the typical individual and the specimen with black ground colour or markings. The term Phæism (φαιός dusky), which applies to dusky specimens, is not so precise in its application and may refer to a case of leucochroism or melanochroism according as the affected individual is more darkly or lightly pigmented than the typical form, without distinguishing the mode by

which the colouring has been arrived at. A modified form of *Helix virgata* var. *rufula*, with the bands present as in the typical form, is an interesting illustration of this phase of colouring (see pl. ii., fig. 3).

Melanism (*μέλᾶν*, black) is the opposite condition to albinism, and is a consequence of the excessive action or hypertrophy of the colour glands diffusing the colouring matter of the bands or other markings over the surface of the shell, and when this diffused pigment is black, or approximately black in colour, the phenomenon is termed melanism. Miss F. M. Hele has observed that certain foods have an influence upon the colouring of growing *Helix aspersa*, as those specimens fed upon lettuce leaves always acquired a darker colour, or the colouring matter became more overspread than was usually the case, and Mr. Standen has also recorded that the sinistral *Helix aspersa* which he fed to maturity upon "dainty food" lost its mottled markings and became almost uniformly black. The coalition of the black bands in *Helix nemoralis*, etc., is a well known and common example of this phenomenon; a still more striking illustration being furnished by the *Helix virgata* var. *nigrescens* (see pl. ii., fig. 2), which has been observed by Mr. Ashford to be a very local form in the Isle of Wight and to live chiefly upon *Carduus tenuifolius*, but Mr. H. B. Hewetson, of Leeds, has found some very characteristic specimens of this variety upon the Ragwort (*Senecio jacobæa*), on the sand-hills at Kilnsea, near Spurn, Yorkshire.

Erythrism (*ἐρυθρός*, red) and Erythrochroism are the terms expressing the development of the red pigment (see pl. ii., figs. 6, 7, 9), and would seem to be a biological expression of a warm climate or season, as we meet with this red form in *Helix nemoralis* and *Helix hortensis* much more plentifully and more richly coloured in the southern counties of England than in the northern parts of the country. This erythrous condition or colouring as existing in the shell of *Helix hortensis* has been considered by Herr Weinland, under certain circumstances, to be protective in character, as for instance, when the animal resides amongst fallen beech leaves, and he has therefore distinguished and named this form the variety *fagorum*, owing to finding the shells in such situations. Xanthous variation (pl. ii., fig. 11) when not pure would seem to be very closely associated or connected with erythrism, and is often developed during growth as a modification of the red colouring existing in early life or *vice versâ*.

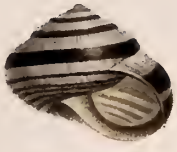


Fig. 1.

Fig 8.

Fig. 9.

Fig. 2.

Fig. 6.

Fig. 10.

Fig. 3.

Fig. 11.

Fig 4.

Fig. 12.

Fig 5.

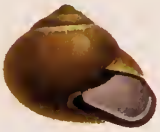


Fig. 7.

Fig. 13.

Principal Phases of Colouring in Mollusca, Figs 1–7 and 11.

TYPICAL. *Fig. 1. Helix virgata Da Costa* × 2, Lewes, collected by M^r T.S. Hillman.
MELANISM. *Fig. 2. H. virgata v. nigrescens Grat.* × 2, Afton Downs, I. of Wight, collected by M^r C. Ashford.
MELANOCHROISM. *Fig. 3. H. virgata v. rufulo-zonata Taylor* × 2, Langharne, collected by M^r G.W. Mellors.
LEUCOCHROISM. *Fig 4. H. virgata v. albicans Grat.* × 2, Newquay, collected by M^r J.H. James.
ALBINISM. *Fig 5. H. virgata v. alba Taylor* × 2, Lewes, collected by M^r C.H. Morris.
ERYTHRISM. *Fig. 6. Arion ater v. rufa (L.)* Minden, Germany, collected by H. Richardson.
ERYTHROCHROISM *Fig. 7. Helix nemoralis v. rubella Picard*, Knottingley, collected by J. Cordukes.
XANTHISM. *Fig. 11. H. nemoralis v. libellula (Risso)*, Winster, collected by Rev. H. Milnes.

Types of Colouring in Thermal Zones, Figs 8–13.

POLYCHROMATISM. (or Tropical colouring) *Fig 8. Liguus virgineus (L.)* West Indies. } M^r E. Collier's collection.
Fig. 9. Helix picta Born. Cuba.
OLIGOCHROMATISM (or Temperate colourings) *Fig. 10. Helix pisana Müll.*, Mentone, collected by M^r R.D. Darbishire.
Fig. 11. H. nemoralis v. libellula (Risso), Winster, collected by Rev. H. Milnes.
MONOCHROMATISM (or Boreal colouring) *Fig. 12. Vitrina pellucida v. depressiuscula Jeffr.* × 3, coll. by M^r E.D. Marquand.
Fig. 13. Vertigo alpestris Alder × 8. Cottingley, Yorks

J.W. Taylor, del. Taylor Bros. Lith. Leeds.

The yellow or xanthous variety, *libellula*, of *Helix nemoralis* is often noticed to present a strong rosy tint upon the earlier or apical whorls, and this peculiarity is occasionally found so distinctly marked that a special varietal name has been used to indicate it.

The *Helix picta* figured (pl. ii., fig. 9) also shows the intimate relationship existing between erythrous and xanthous colouring, as both colours are blended together upon the penultimate and preceding whorls. Indeed the shell, like other organs of the body, undergoes in some species great mutations, in colour, as well as in markings and other characters in the progress of its growth to maturity.

The real colour of the shell is sometimes greatly modified to the eye by the colour of the chitinous periostracum, which may vary from the pure white of the albine form, through the delicate primrose tint of the xanthochroic varieties, as seen in *Helix arbustorum* and *Helix aspersa* (see pl. i., fig. 1), to the deep dark brown, as found in *Helix aculeata* and other species, and according to its depth of tint and thickness obscures and modifies the colour of the calcareous surface beneath; thus some of the yellowish brown and other varieties of *Helix nemoralis*, etc., when denuded of their epidermis are found to be of a more or less intense and livid violet colour, but other Univalve species may chiefly or entirely owe their colouring to the chitinous covering of the shell.

The Banding, or coloured markings, in our British Univalves have usually a spiral character, the corresponding markings in the Bivalves being those radiating from the umbones to the free margins of the shell, thus differing diametrically from the general direction of the sculpture, which is usually transverse or coincident with the lines of accretion. These varied markings are formed by the glands of the mantle margin, and their continuous exercise during growth produces a connected and necessarily spiral band in the Gastropoda, and the radiate markings in the Pelecypoda, their intermittent action giving rise to transverse markings, spots, or blotches according to the extent of the development of the colour glands and the greater or lesser intervals taking place between the periods of their secretory activity.

Mr. W. H. Dall has remarked that the tendency to striped markings would probably aid in the concealment of the shells amongst the lights and shadows of the grass and herbage, leading one to attribute these markings to similar causes to those that may have also led to the development of the striped markings of the Tiger.

Rev. S. Spencer Pearce, on the contrary, attributes the development of distinct banding, in species such as *Helix caperata*, to the greater visibility of the shells so marked to those with mottled or indistinct markings, as he found that the strongly banded variety *ornata* preponderated in the places fed over by sheep, which he therefore assumed perceived and avoided the striped form, whose markings would thus appear to be of a warning or aposematic character, while probably destroying many of the less conspicuous, indistinctly banded specimens. In the hedge-rows and other places not browsed over by the sheep, the ordinary mottled form prevailed and the distinctly striped variety was comparatively rare.

FIG. 193.—*H. caperata* Mont., Perth,
Collected by Mr. H. Coates,
Probably largely destroyed by sheep owing to its indefinite and protective colouring.

FIG. 194.—*Helix caperata* var. *ornata* Picard,
Afton Downs, Isle of Wight,
Collected by Mr. Chas. Ashford,
Probably avoided by the sheep, the distinct markings enabling the shells to be easily perceived.

Some species have normally a definite number of bands, the group *Pentatænia*, to which *Helix nemoralis*, *hortensis*, *pomatia*, and *aspersa* belong is characterized by possessing five bands in the typical form, which are very constant in position, three being always above the periphery and two below it, but they are subject to great modification, owing to the absence of one or more of the bands and to their coalescence in many and varied combinations.

Simroth from his study of slug colouration was led to regard the second and fourth bands of the *Pentatænia* as the primitive and original pair—corresponding to the ancestral mantle-bands of the slugs, which are closely connected with the lateral blood sinuses—which, by the concentration of their pigment, have acquired a lighter border on each side, throwing up the third band between them, and each developing an additional one outwardly, the first and the fifth. This view is scarcely borne out by the acknowledged fact, that the third band in *Helix nemoralis*, when present at all, is the band which first appears upon the infant shell, and therefore implies for it an earlier origin than for the remainder.

A convenient method or formula was devised many years ago by Herr Georg von Martens to facilitate the tabulation and record of the band variations in the *Pentatænia*, for which purposes the character of the banding should always be taken from the last whorl of the shell, as the markings so often vary in character during

the progress of growth, the banding being usually isolated and distinctly separate in youth and tending to become transversely combined at the margin of the aperture on approaching maturity. By this method a distinctive or special number is applied to each of the five bands found in the typical form of *Helix nemoralis*, or other species of the Pentatæniate group, according to the position it occupies on the shell, the uppermost or one nearest the suture being the first, and the lowermost or one nearest the umbilicus the fifth, the type form, which has always five distinct bands, being expressed by the formula 12345 (see f. 195).

Fig. 195.—*Helix nemoralis* L. type formula 12345, Bitton, near Bath, Collected by Miss F. M. Hele.

If a band is suppressed or absent, this is shown by the use of a cypher 0 instead of its number; thus the formula 12045 would signify that the first, second, fourth, and fifth bands were present, and the cypher in its appropriate position would indicate the absence of the third band (see f. 196); if, however, the whole of the five bands are absent and the shell be therefore practically unicolourous from showing only the ground tint, then this phase of variation is expressed by the use of five cyphers 00000 in lieu of the appropriate numbers (see fig. 197).

Fig. 196.—*Helix nemoralis* L. formula 12045, Bitton, near Bath, Collected by Miss F. M. Hele.

Fig. 197.—*Helix nemoralis* L., formula 00000, Isle of Lismore, Argyll, Collected by Mr. A. Somerville, B.Sc., F.L.S.

The coalescence or fusion of the banding is indicated by enclosing in parentheses, or by some other method which will clearly show the peculiarity, the numbers representing those bands which are united together, thus the formula (12) 3 (45) would signify that the first and second bands were united, and also the fourth and fifth, the third only being free or isolated (see f. 198).

Fig. 198.—*Helix nemoralis* L., formula (12) 3 (45), Piperstown, co. Louth, Collected by Miss S. Smith.

When, however, the whole five bands are present and united together, presenting the appearance of one excessively broad band occupying nearly the entire surface of the whorl, and therefore only

allowing the ground tint to be visible along the suture and in the umbilical region (see fig. 199), this is shown by enclosing the whole of the five figures within the parentheses, the formula being (12345).

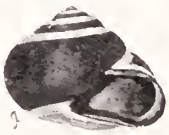


Fig. 199.—*Helix nemoralis* L., formula (12345), Truro, Cornwall, Collected by Mr. J. H. James, A.R.I.C.

Supernumerary or extra bands may also apparently be developed, so that a specimen may seem to have six, seven, or more bands, but these additions to the normal five, are invariably owing not to a real increase in their number, but to the separation or splitting up of one or more of those normally existent, and consequently these extra or supernumerary bands are always finer and thinner than the normal undivided band would have been. This splitting up or sub-division of the bands can be indicated in the formula by the use of a smaller figure placed in such a position as to represent the situation actually occupied relatively to the regular banding by the slender split-off bandlet : thus, if the third band be split about equally, it should be indicated by $12^{3}345$ (see fig. 200), or if the split-off bandlet is much narrower than the remaining portion of the band from which it has been separated and is placed beneath it, the formula should be $123^{4}45$ (see fig. 201), but if the bandlet be placed above the band it is derived from, the smaller figure, by the position it occupies, equally serves to indicate its position and character, the formula being $12^{3}345$ (see fig. 202).

Fig. 200.—*Helix nemoralis* L., formula $12^{3}345$.

Fig. 201.—*Helix nemoralis* L., formula $123^{4}45$,

Fig. 202.—*Helix nemoralis* L., formula $12^{3}315$,

In those cases where, from their equi-distant position, it is difficult or impossible to decide with certainty from which of the normal bands the extra bandlets have been derived or split off, so that the appropriate numerals cannot be used to indicate their position and origin, then a small × is used instead of a number in the proper position to indicate their presence, thus

Fig. 203.—*Helix nemoralis* L., formula 123×45,

a specimen as the one figured (fig. 203), which possesses a slender bandlet equidistant between the third and fourth bands, would be clearly indicated by the formula 123×45.

Indistinct, irregularly developed or spotted bands are indicated by a colon in place of the numeral—an indistinct third band, provided the remaining four bands are normally developed, would be shown by the formula 12:45; whereas if all the bands are indefinite or irregular, the peculiarity would be expressed by the use of the formula :::::, as in fig. 204. Some authors, however, consider that any of the normal bands when indistinct or rudimentary are more suitably indicated by the use of the small numeral, which I recommend should be restricted to represent the split-off bandlets.

Fig. 204.—*Helix nemoralis* L., formula :::::, Spurn Point, Yorkshire, Collected by Mr. W. E. Clarke, F.L.S.

A specimen of *Helix hortensis* from Folkestone, kindly given me by Mrs. Fitzgerald, appears to have eight slender but distinct bands, on account of their colouring matter being mainly concentrated at the edges of each band, leaving the centre of each band very little, and in some portions not at all darker than the general ground colour, this separation of the margin of the bands gradually becoming more distinctly marked as growth proceeds, and furnishing a very instructive illustration as to how the multiplication of bands may come about, this specimen would be indicated by the formula $12^{3}3^{4}4^{5}5^{6}$ (fig. 205).

Fig. 205.—*Helix hortensis* Müll., formula $12^{3}3^{4}4^{5}5^{6}$, Folkestone, Kent, Collected by Mrs. Fitzgerald.

This division of, or breaking up of the banding is a modification which has been ascribed to the effects of aridity or dryness, either of season or locality, and that this cause probably induces band disintegration, is shown by the fact that Mr. W. E. Clarke collected for me, at Whitsuntide, 1882, several thousands of *Helix nemoralis* from the sand-hills at Spurn Point, Yorkshire, a locality which, according to the meteorological reports, is one of the driest spots in the kingdom, and it is remarkable that not a dozen of the immense number gathered exhibited evenly developed and strongly marked banding, the bands when present were all more or less broken up and disconnected (see fig. 204) and this circumstance furnishes modified evidence of the evolution of bandless species in desert districts; this

snsceptibility to climatic or meteorological influences has been termed Horæomorphism.

The character of the banding sometimes changes very markedly dnring growth in some individnals. In the early whorls the bands may be quite separate and distinct, and afterwards become gradnally united together as the termination of growth or matnrity is approached; this change arising from the excessive development or hypertrophy of the colour glands of the mantle.

Fig. 206.—*Helix nemoralis* L. × 1½, Church Fenton, Yorks., Collected by Mr. W. D. Roebuck, Showing the tendency of the banding to become confluent at the aperture of the shell.

This transverse coalition of all the bands may also take place towards the completion of each little stage of growth, each recommencement exhibiting a practical atrophy of the colour glands or at least a temporary failnre of their fnnction, and also a rapid resumption of excessive secretive power. This rhythmical alternation of the hypertrophy and practical atrophy of the colour glands of the mantle margin resnlts in the form of *Helix nemoralis* which has been called the variety *undulata* by Gentilnomo.

Fig. 207.—*Helix nemoralis* var. *undulata* Gentiluomo × 1½, Blagdon, near Bristol, Collected by Miss F. M. Hele, Showing the alternation in the secretive power of the colour glands forming the banding.

The more or less complete permanent atrophy of the glands forming the banding may, however, occasionally take place at the termination of one of the periods of growth, before the maturity of the shell, the growth afterwards made being wholly or partially deficient of the banding, distinctly present on the preceding whorls.

Fig. 208.—*H. hortensis* Müll., Frutigen, Switzerland, Showing the abrupt cessation of the normal banding.

In other cases, on the contrary, the secretory power of the glands may be nndeveloped or dormant during growth, and gradually, or more rarely suddenly develop in full strength as maturity and the period of fullest vigour is approached.

Fig. 209.—*Helix pisana* Müll. × 1½, Tenby, South Wales, Collected by Mr. J. R. B. Masefield, M.A., Showing the abrupt commencement of distinct banding.

The flammnlar or flame-like markings are those which are somewhat irregularly shaped and may be considered to frequently originate from a disintegration of the primitive spiral or longitudinal

banding, both in shells and slugs, and transverse markings may have often arisen from the re-aggregation of these spots in the direction more or less perpendicular to that in which they were primitively present, but it is not unlikely that irregularly spotted band-like markings indicate irregularity of action, such as may be looked for at the origin of such glands, and thus occasionally represent nascent banding and not invariably originate from primitively distinct and continuous markings.

FIG. 210.—*H. aspersa* var. *flammea* Pic. × 1½,
Scarborough, Yorks.,
Collected by Mr. J. Ray Hardy,
Showing disintegrated or flammular banding.

Helix cantiana, *Helix cartusiana*, *Helix rufescens*, and a few other species, although normally uniformly coloured, occasionally exhibit unmistakable traces of spiral banding, which some assert are nascent, but are more probably the vestigial remains of bands formerly existent; and we are thus led to speculate upon the probability of these species being at one time distinctly banded forms, and descended from primitively banded ancestors, without, however, implying that the molluscan shell, as originally developed, was not unicolorous. The evidences of this banding are rendered easily recognizable by the pale peripheral zone, which is, according to my interpretation, the intervening area between the upper and lower groups of bands.

FIG. 211.—*Helix cantiana* var. *albocincta* Ckll.,
Lund, near Osgodby, Yorks.,
Collected by Mr. Wm. Nelson,
Showing supposed atavistic evidence of spiral banding.

The whitish transverse linear markings, which form the characteristic feature of *Limnæa palustris* var. *zebra*, are, I am inclined to believe, the result of a certain amount of disintegration of the shell substance, which apparently takes place at somewhat regular intervals, owing probably to some periodically recurring deficiency in the secretion of the protective epidermis. Analogous markings from similar causes are sometimes noticed upon *Bythinia tentaculata* and other species, but this feature is apparently more particularly a characteristic of the *Limnophysa* inhabiting North America.

FIG. 212.—*Limnæa palustris* var. *zebra* Tryon × 2,
"Swale," Oakland Co., Mich., U.S.A.,
Collected by Mr. Bryant Walker,
Showing regular transverse linear markings, perhaps due to disintegration of shell substance or defective periostraca.

The Spiral White Lines so often noticed, especially in our fresh-water shells, are not usually what may be termed true colour bands, as those of typical *Limnæa peregra* var. *picta* are said to be, but are probably the result of some injury to the glandular mantle-margin, which interferes with the secretion and deposition of the usual epidermic covering to the outer surface of the whorls, thus rendering the calcareous strata of the shell more vividly perceptible. Mr. L. E. Adams has frequently noticed this peculiarity amongst the *Limnæa peregra* inhabiting Scout Dam, near Penistone, Yorkshire, where trout are very numerous, and I consider these markings are probably caused indirectly by the fish, which have injured or lacerated the mantle with their teeth when attempting to seize and feed upon the animal. More severe injuries of this character, from the same or other causes, would probably result in the entire thickness of the shell substance being more or less affected, and in extreme cases the outer margin of the shell, where the new growth takes place, might even become cleft.

Fig. 213.—*Limnæa peregra* (Müll.) × 1½.
Scout Dam, Penistone, Yorks.,
Collected by Mr. L. E. Adams, B.A.,
Showing the spiral linear markings, probably due to injury to mantle-margin.

Figs. 214 & 215.—*Limnæa auricularia* L.),
Davos Lake, Switzerland,
Collected by Capt. W. H. Turton, R.E.,
Showing cleft shell substance probably due to severe laceration of mantle-margin.

In the Pelecypoda the same peculiarities are occasionally observable, the radiating dull white linear markings, when present, corresponding to the linear spiral markings of the *Limnæidæ*, etc., and are very probably attributable in origin to analogous causes.

More severe injuries to the mantle, would, as in the Univalves, result in the complete severance of the substance of the valve, but this severance is seldom so strikingly shown as in the specimen of *Anodonta cygnea* figured, which has the left valve cleft almost to the umbo, owing to the severe injury the corresponding mantle has sustained in early life, but the right valve shows only a very marked constriction to indicate the extent of the injury done.

These malformed shells should more properly have been treated upon in the succeeding chapter, but the desire to indicate the probable connection of such forms with those distinguished by the

development of spiral or radiate dull white lines, make it desirable that these peculiarities should be treated of under this head.

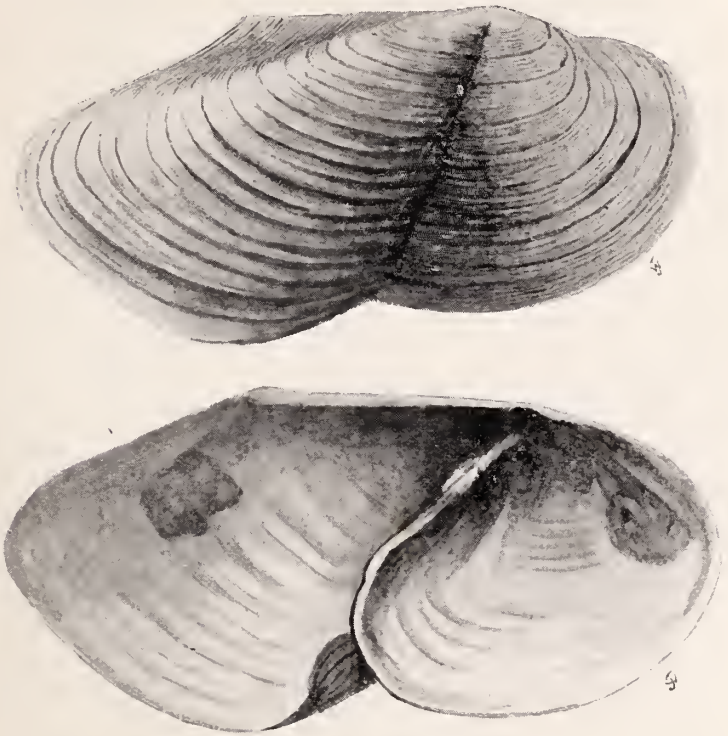


FIG. 216.—*Anodonta cygnea* (L.),
Sandwill Park, Staffordshire, collected by Mr. J. Madison,
Showing the effects of some severe laceration of the mantle, the result of which is seen in the strongly separated parts of the left valve and in the deeply-furrowed right valve.

MONSTROSITIES.

Monstrosities are generally considered to be those individuals whose differences arise from pathological causes; the name is likewise very appropriately applied to those malformations which may be congenital and transmissible from one generation to another, as is sometimes the case with the reversed monstrosities, although M. Sanier, who endeavoured to perpetuate the reversed form of *Helix aspersa* by accumulating several adult specimens and breeding from them, found the few resultant progeny all dextral, and this experience has been confirmed by others. The term monstrosity also indicates specimens which have become deformed during growth, owing to some intrinsic or extrinsic irritation or disturbance, perhaps causing

irregularity in the secretive power of the animal, and the correlation which doubtless inseparably exists between the form and character of the shell and the organs of the body renders it very probable that abnormality generally, indicates or is associated with, such functional disturbances or differences as are detrimental to the creature and tend to its more easy destruction by its enemies, or by any unfavourable conditions to which it may be exposed. The researches of Mr. R. E. Call upon the relative abundance or rarity of the sinistral monstrosity of *Melantho* in the embryonal and the adult stages are very significant, and show that the mortality amongst the sinistral specimens is strikingly greater than amongst those normally coiled, and would appear to corroborate the presumed general physiological weakness of abnormal specimens. It is, however, sometimes difficult to discriminate between a true variation and a monstrosity, but malformations or monstrous growths seldom occur in the embryonal stages, and an examination of the nucleus of the shell, whether Univalve or Bivalve, generally offers a clue to distinguish these accidentally malformed shells, as they frequently only develop the abnormality after the commencement of a free life—in fact, monstrosities generally may be considered to be the more extreme examples of accidental variation, and their study is useful as tending to elucidate the range of specific variability.

Unhealthy or unnatural conditions of life would appear to disorganize the animal functions, with the effect that the resultant growth is often irregular or abnormal in appearance and character. A stream of water pumped from a colliery at Leventhorpe Pastures,

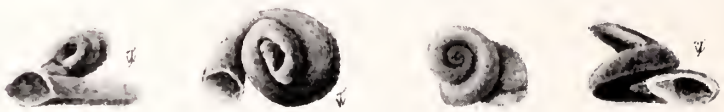
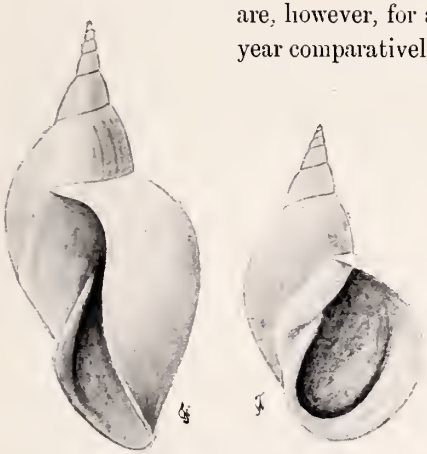


Fig. 217. Fig. 218, Fig. 219, Fig. 220.

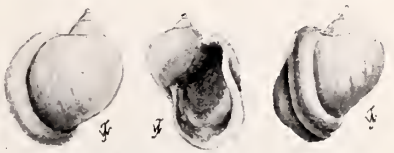
Planorbis carinatus Müll. (enlarged),
Pit stream, Leventhorpe Pastures, Leeds, collected by Mr. Jas. Beevers,
Dorsal and side views of two individuals showing the grotesque and irregular coiling assumed to be the effect of abnormal conditions.

near Leeds, yielded a very large number of curiously twisted shells of *Planorbis carinatus*, of which a large proportion were sinistrally coiled, and all of which were thickly encrusted with a dense black carbonaceous deposit. So universally prevalent were these remarkable shells in this stream, that at one time it was a rarity to obtain a normally coiled specimen.

In the saline marshes in the vicinity of the Sea of Aral, which are, however, for a considerable period of each year comparatively fresh, Mr. W. Bateson, M.A., found specimens of *Limnæa stagnalis*, *L. auricularia*, and *Limnæa peregra*, some of which appear to have undergone a certain degree of modification, doubtless owing to the exceptional character of the environment: through the kindness of the Rev. A. H. Cooke, M.A., I am enabled to give several illustrations of *Limnæa stagnalis* and *Limnæa auricularia*, which will serve to illustrate the change in form and character the peculiar features of the region has induced. It is interesting to notice the comparatively slight effect the abnormal conditions have produced in the *Limnæa stagnalis*, which are fine and well-grown shells; the unusual environment is, however, much more strongly indicated by the *Limnæa auricularia*, which are dwarfed and curiously malformed towards the aperture, thus confirming the results of Beudant's experiments, which showed *Limnæa auricularia* to be more sensitive than *Limnæa stagnalis* to the influence of saline water.



FIGS. 221, 222.—*Limnæa stagnalis* (L.), Salt Marshes, Sea of Aral, Collected by Mr. W. Bateson, M.A., Showing the result of living in periodically saline or brackish waters.



FIGS. 223, 224, 225.—*Limnæa auricularia* (L.), Salt Marshes, Sea of Aral, Collected by Mr. W. Bateson, M.A., Showing the result of living in periodically saline or brackish waters.

Univalves generally, often become ribbed, keeled, or otherwise more or less irregularly modified by the influence of an influx of brackish or saline water. In the Miocene Tertiaries of Asia Minor, Prof. Forbes found whole races of *Neritina*, *Viripara*, and *Melanopsis* with the whorls ribbed or keeled, as if through the unhealthy influence of an influx of this character.

The refuse of a chemical factory was prior to 1887 turned into the lake in Drinkwater Park, near Prestwich, and the effects of this

pollution of the water was reflected in the *Limnæa stagnalis* found there, which exhibited somewhat swollen transverse growths near the mature aperture and the growth lines were altogether ruder and stronger in character than in ordinary shells. The following year, when the pollution of the water by this chemical refuse was stopped, the succeeding generation of shells quickly indicated and reflected the greater purity of the water by a reversion to the regular outline and smooth even surface of normal shells.

FIG. 226.—*L. stagnalis* (L.), Lake, Drinkwater Park, near Prestwich, Lancashire, Collected by Mr. W. H. Heathcote, F.L.S., Showing by irregular growth the baneful influence of the chemical refuse formerly discharged into the lake.

Species usually inhabiting tranquil or gently flowing waters tend to become deformed and dwarfed if subjected to the influence of strong currents; this is strikingly exemplified in *Unio tumidus* found in the river Foss, near York; the specimens found close by the overflow or bye-wash of the Yearsley Locks, within the influence of the current, being greatly dwarfed and malformed in their growth, differing very markedly from the symmetrically formed and fairly-sized shells frequenting the sluggishly flowing river a short distance away; such agitated waters are also usually correlated with an increase in

FIG. 227.—*Unio tumidus* Phil., Yearsley Lock, near York, Collected by Rev. W. C. Hey, M.A., Showing the dwarfing and distortion of the shell owing to proximity to the dam.

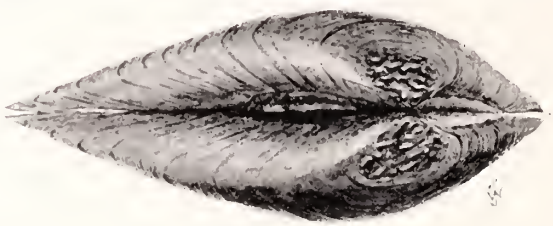


FIG. 228.—*Unio tumidus* Phil., Near Yearsley Lock, River Foss, York, collected by Rev. W. C. Hey, M.A., Showing the ordinary form as found a short distance from the dam, in gently flowing waters.

the strength and development of the hinge-teeth or denticles, which are liable to become feeble and degenerate in quiet and unruffled waters.

Dr. A. Brot has shown how some of the lowliest organisms may influence even the form of the shell in the mollusca, as he records that during one season nine-tenths of the specimens of *Limnæa peregra* living in a pool near Geneva, were curiously malformed at the base of the columella and anterior part of the shell generally; this malformation, which was correlated with a certain dwarfing of the shell, was concurrent with an extraordinary abundance of *Hydra viridis* in the same pond. The following year the *Hydra* had disappeared, and this disappearance of the *Hydra* was coincident with the disappearance of the peculiarity in the shell, of which the *Hydra* was apparently the primary cause, as the succeeding generations of the *Limnæa* were quite normal.

FIGS. 229, 230, 231.—*L. peregra* (Müll.) × 1½,
A pool, near Geneva,
Collected by Dr. A. Brot,
Showing the deformation of the columella and the base of shell, assumed to be caused by *Hydra viridis*.

FIG. 232.—*L. peregra* (Müll.) × 1½,
A pool near Geneva,
Collected by Dr. A. Brot,
Showing the normal form as found in the pool with the malformed individuals.

Herr Julius Hazay has also observed and recorded that the "invasion" of the shell by the leech may greatly influence the character of the growth in *Limnæa stagnalis*, by causing the animal to gibbously inflate the outer margin of the aperture of its shell on attaining maturity.

FIG. 233.—*Limnæa stagnalis* (L.),
Buda-Pesth,
(after Herr J. Hazay),
Showing the inflected lip, said to be owing to the "invasion" of a leech.

Dreissensia polymorpha, like other attached shells, is liable to malformation, owing to interferences during growth, consequent upon their situation in crevices and from contact with hard substances. This species also often causes distorted and irregular growth in *Anodonta* and other freshwater bivalves, by fastening their valves together with its byssus.

It has been stated by Prof. Alphæus Hyatt that distortions of Univalve freshwater shells have usually occurred in still, enclosed waters with no outlet, and, although this is generally, it is far from being universally true.

The Sinistrorsity and Dextrorsity of the molluscan shell is a very intricate and perplexing subject, which in some genera has given rise to considerable discussion. The great majority of Gastropoda have undoubtedly dextral shells, that is with the whorls turning spirally from left to right, with the heart on the left side of the animal, and the external apertures of the various organs on the right. The sinistral or left-handed coiling is thus the exception or monstrosity, although some species and even genera are normally sinistral, and possess an opposite arrangement of their internal organs to dextral species, and the dextrally coiled shell becomes the exception or monstrosity. Reversed monstrosities likewise conform to this disposition of the viscera, a dextral monstrosity of a normally sinistral shell having its organs and orifices disposed as in those mollusks which are normally dextral. This reversal of the direction of the coiling, though liable to occur in all spiral shells, is of much greater rarity in some species than in others—for, of *Helix rotundata*, our commonest species of *Helix*, only one recent sinistral specimen is known, which was found by Rev. H. W. Lett, at Loughbrickland, in the north of Ireland, and through his kindness is now in my collection.

All mollusks with spiral shells are liable to this reversal in the direction of their convolution, and bivalves and even slugs are affected in an analogous way. In bivalves the right or left valves, as the case may be, acquire the characters which normally distinguish the other, but this reversal when it does occur is not very noticeable except perhaps in some of the inequivalve species. In the naked genera, the occurrence of this state is outwardly shown by the transference of the respiratory and other orifices to the side opposite to that on which they are normally placed.

Locality would appear to have some influence in inducing the reversed coiling of shells, some localities being well-known for the regular recurrence of these monstrosities, while in other districts they are scarcely known to occur. Cailliaud records the neighbourhood of Rochelle as noted for the frequent occurrence of sinistral *Helix aspersa*, and Dr. Gwyn Jeffreys states that he himself saw a colony of that monstrosity in the garden of M. d'Orbigny in that city.

A sinistral race of *Helix nemoralis*, almost analogous to that formerly existent of *Fusus antiquus*, would appear to have at one time lived in county Donegal, as the very numerous subfossil shells picked out of the immense sand-hills about Bundoran abundantly testify.

The causes of this reversal of the normal arrangement are however not at all known or understood. M. Bourguignat has hazarded the suggestion that it may be caused by electrical conditions, the electric current flowing in the opposite direction to the embryonal rotation, the essential conditions being a metalliferous soil, moist weather to influence the latent electricity of the metallic substances, and the conjunction of the atmospheric and terrestrial electricity, as by thunder at the period of the first manifestation of vitality by the embryo. Prof. Carus also considers that the direction of the coiling of the shell and animal may possibly be determined by the direction of the embryonal rotation.

Mr. R. Ellsworth Call attributes sinistrorsity in *Melantho* to the crowding of the embryos in the oviduct in the early stages of their existence; his observations on that genus lead to the inference that sinistral specimens are more delicately constituted than their normally coiled brethren, as he found that sinistral examples constituted $1\frac{1}{2}$ per cent. of the total number of the embryos in the oviduct of *Melantho integra*; and $2\frac{1}{2}$ per cent. in *Melantho decisa*, while judging from the numbers gathered in the adult stage, he found only one-tenth per cent. survived.

In *Limnæa* Mr. H. E. Crampton, jun., has recorded that the direction of the cleavage during segmentation of the ovum, is of the typically spiral type, but in *Physa* the direction of this cleavage is totally reversed. Dextrorsity and sinistrorsity are however qualities inherent to the organization of the animal, and the particular arrangement is usually correctly indicated by the position of the heart and the external orifices of the reproductive and other organs of the body.

Fig. 234.
Exogastric coiling.

Fig. 235.
Endogastric coiling.

Diagrams showing the process by which an Exogastric mollusk becomes Endogastric by the torsion of the visceral sac through an arc of 180°, a process determining the sinistrorsity or dextrorsity of the shell (after Pelseneer). *a*. anus.

(The figures, for the sake of clearness and intelligibility, are drawn to represent a much later stage of embryonal development than that at which the torsion actually occurs.)

All embryonal Gastropods are primitively what are termed Exogastric, and only become Endogastric owing to the torsion of 180° which is undergone by the visceral sac, which twisting transfers the anus and other organic orifices from the rear to the anterior part of the animal; the incipient spire at first enrolled towards the front or dorsally with reference to the later whorls, becoming coiled towards the rear. According to Prof.

Pelseneer there are no adult Gastropods which are coiled exogastrically, but amongst the Cephalopods the *Nautilus* furnishes an example of this primitive arrangement. The original sinistrorsity or dextrorsity of the coiling is determined by the method in which this torsion is effected: if twisted to the right the shell or coiling is dextral, if to the left, sinistral, but the direction of the torsion is naturally correlated with the arrangement or disposition of the vital organs of the body.

If we are correct in applying the same terms to the Pelecypoda, and considering as the same phenomenon the slight tendency to coiling exhibited by our freshwater Bivalves and more unmistakably by some marine forms as *Isocardia*, etc., then we may regard all our British species as Exogastric or PROSOGYRATE forms, as the apices of their valves are directed anteriorly. None of our freshwater species, and only a limited number of marine forms, as *Donax*, *Trigonia*, etc., are really Endogastric or OPISTHOGYRATE, that is with the umbones directed towards the posterior margin of the shell.

Rev. Leonard Jenyns in his monumental and classical work, "A Monograph on the British Species of *Cyclas* and *Pisidium*," has unfortunately erroneously figured all the *Pisidia* therein as Opisthogyrate or Endogastric, with the apices of the valves directed towards the shorter or posterior margin, instead of to the longer or anterior one, as they undoubtedly are: this difference can be strikingly seen

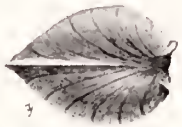


FIG. 236.—*Pisidium henslowanum* (Shepp.), adult, posterior end, × 12,
Pond, Cockerton, Darlington,
Collected by Mr. Charles Oldham,
Showing the endogastric or prosogyrate direction of the umbones.

FIG. 237.—*Pisidium henslowanum* (Shepp.), young, magnified (after Jenyns),
Showing, though erroneously, an exogastric or opisthogyrate direction of the umbones.

by reference to, and comparison of my figure of *Pisidium henslowanum* (fig. 236), with fig. 237, which is faithfully reproduced from a figure in Mr. Jenyns' Monograph.

HYPERSTROPHY (*ὑπέρ*, above; *στροφή*, turn).—Although sinistrally or dextrally coiled shells are usually inhabited by animals sinistrally or dextrally organized, as the case may be, yet exceptions are known in which a sinistrally organized animal is the tenant of an apparently dextrally coiled shell, and *vice versâ*; this curious feature which is exhibited by the genus *Planorbis*, has always been a fruitful source of discussion amongst conchologists, some contending that

Planorbis is a dextral shell, others affirming it to be sinistral, whilst a few, including the celebrated Lamarck and Deshayes, were disposed to view the genus as amphidromic, some species in their opinion being dextral and others sinistral in character. The apparent anomaly is, however, ingeniously and satisfactorily explained by the hypothesis of hyperstrophy, which makes clear the origin and derivation of these puzzling shells, which are in apparent disagreement with their inmates and architects. The hyperstrophic theory may be explained by imagining a homœostrophic or orthostrophic shell as *Physa*, which is sinistrally coiled and is inhabited by a sinistrally organized animal, to have its spire gradually shortened until the shell becomes discoid, owing to the spire sinking to the level of the body whorl, as in *Planorbis*, and if the process be further continued the spire protrudes at the opposite side, as in the genera *Pompholyx*, *Carinifex*, etc., all of which are sinistrally organized animals, but by the change described now inhabit apparently dextral shells.

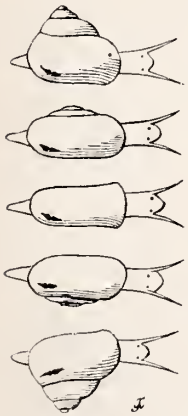


Fig. 238. An orthostrophic sinistral shell, as *Physa*, showing the heart at base of whorl.

Fig. 239. Intermediate, subdiscoidal, sinistral form.

Fig. 240. Discoid form, as *Planorbis*.

Fig. 241. Intermediate, subdiscoidal, pseudo-dextral form.

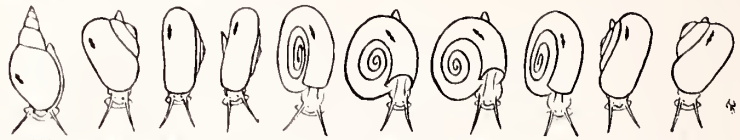
Fig. 242. A hyperstrophic pseudo-dextral shell, as *Pompholyx*. The heart is now seen to be at spire side of body whorl.

Diagrammatic figures showing in a conventional and simple way the change from an orthostrophic sinistral shell to a hyperstrophic pseudo-dextral one.

The terms Inversion or Hyperstrophy serve to indicate this change by which the part originally forming the base of the shell in its normal or primitive position becomes the upper or spire face and *vice versâ*, this process also apparently reversing the direction of the coiling of the shell, although this reversal is arrived at in a totally different way and does not affect the disposition of the organs of the animal, as does a simple reversal of the coiling, which always involves the transposition of the various organs of the body, those organs normally placed on the right side of the animal being transferred to the left side, and *vice versâ*. Sinistrorsity or dextrorsity by inversion or hyperstrophy is therefore essentially different from sinistrorsity or dextrorsity arising from a simple reversal in the direction of the convolution of the shell. In the former case, although the mode of coiling has been modified, the animal retains the usual arrangement

of its viscera, but the basal part of the shell becomes by transposition of hyperstrophic growth the upper or spire face ; in the latter case, it is the organs of the animal that become actually transposed in position, those upon the right side become placed on the left, and *vice versâ*, but the shell is simply reversed in its direction of convolution, the basal and upper faces of the shell retaining their positions as in the normal individuals, and are not transposed as in hyperstrophic specimens.

Theoretically, there may thus be four different phases in the coiling of Planorboid shells. Viewing the shell of *Planorbis* as being now dextral, they may be simply sinistral or simply dextral, or sinistral or dextral by atavism, although only three of these phases are actually known, the simply dextral and simply sinistral forms, and the atavistically sinistral.



Figs. 243, 244, 245, 246, 247, 248, 249, 250, 251, 252.

Diagrammatic figures showing the probably **actual** mode by which the change from a sinistral orthostrophic shell to a hyperstrophic and pseudo-dextral one has taken place. The heart is seen to apparently move from the base to the upper part of the whorl.

In the series of figures preceding, I have endeavoured to depict diagrammatically the gradual and actual mode by which the pseudo-dextral (or ultra-sinistral, as they are sometimes though less happily termed) shells of *Pompholyx*, *Planorbis*, etc., have probably arisen. The fig. 243 is assumed to represent an elongated *Physa* carrying its shell with the apex directed to the rear as is normal ; the actual and particular mode of carrying the shell by the different species, is doubtless always determined by the mechanical laws governing its easiest portability in the medium in which they live. Fig. 244 is an intermediate or transitional form, which finds its original among some of the foreign genera. Figs. 245—247 may all be regarded as more or less faithfully representing *Planorbis corneus*, as the spire is still slightly exserted on the left side, and the shell carried nearly upright as is usual. Figs. 248 and 249, which show hyperstrophic development a little further advanced, also demonstrate how upon any relaxation of muscular effort by the animal the shell falls naturally into a more or less horizontal and truly dextral position. Figs. 250 and 251 show the process advanced a stage further as in *Planorbis*

contortus, the spire now showing on the right side, and leading to *Pompholyx* (fig. 252), which represents one of the extreme pseudo-dextral or ultra-sinistral forms. In the series of figures illustrating these marvellous changes, the heart can be seen in the orthostrophically sinistral *Physa* to be towards the base of the whorl, and it is instructive to note the change in its position in reference to the shells being placed towards the upper or spire face of the whorl in the hyperstrophic individual, and this without any change in its position amongst the viscera of the animal. The orifices of the reproductive and other organs in all these forms continue upon the left side.

The shell of *Planorbis* having become practically dextral, or as it may perhaps be more correctly termed pseudo-dextral, as indicating its hyperstrophic origin from a shell primitively sinistral, has naturally assumed some of the modifications especially distinguishing the truly phylogenetically dextral shells, the right or primitively basal side of the aperture having by the inversion of the shell become the upper side, has acquired the characters suitable to its new position and become more advanced in growth, as the upper side usually is (see page 25, fig. 31). Fischer and Bouvier, who assert that the anterior or basal part of the aperture in *Limnæa* and *Physa* is the most advanced in growth are incorrect in this and in the deductions they derive therefrom.

FIG. 253. — *Planorbis marginatus* m. *cochlea* Brown × 3, Risegate Eau, Gosberton, Collected by Mr. H. Wallis Kew, F.Z.S.,

Showing the pseudo-dextral shell, with the keel sub-basal, indicating a sinistral organization of the animal.

FIG. 254.—*Planorbis spirorbis* monst. *priscum* Taylor × 8, Clay pond, Gorton, Manchester, Collected by Mr. J. Ray Hardy,

Showing atavistic reversion to the primitive sinistral direction of coiling, the keel indicating the sinistral organization of the animal.

The interesting specimen of *Planorbis spirorbis* figured, is sinistrally coiled and the elevated or subdorsal position of the keel testifies that if the normal shell be considered as dextral or pseudo-dextral in accordance with its position upon the animal, we have here an actual instance of atavic reversion to the original direction of convolution; in fact, a reversal of the process by which the pseudo-dextral shell of *Planorbis* has been arrived at. The rarity of what I venture to term the atavistically sinistral form and the comparative frequency of the dextrally spiral monstrosity

would appear *primâ facie* to clearly establish this latter direction as having now become the normal one for the coiling of the shell.

The specimen of *Planorbis carinatus* from Leventhorpe Pastures, Leeds, is an example of sinistrorsity arising from a simple reversal of the now normal method of convolution, and not from an atavistic reversion to the primitive type, as in the *Planorbis spirorbis* (f. 254); this is clearly attested by the position of the keel, which is distinctly sub-basal as in the pseudo-dextral typical form, and shows that the animal forming it, was dextrally organized, as the keel always corresponds with and indicates the side of the anus and other organic orifices.

Fig. 255. — *Planorbis carinatus* monst. *sinistrorsum* Taylor × 1½, Leventhorpe Pastures, Leeds,
Showing a simple sinistral reversal of the now normal pseudo-dextral coiling, the position of the keel indicating the inmate to be dextrally organized.

The nervous system offers confirmatory evidence of the sinistral character of the organization of the animal of *Planorbis*, by the comparatively enormous development of the left visceral ganglion, which disparity in size, in comparison to the corresponding ganglion of the right side, is mainly owing to its innervating the special sense organ—

Fig. 256. — Nerve ring of a half-grown *Planorbis corneus* (L.), with cerebral commissure cut and the cerebral ganglia thrown back, showing the sinistral organization of the animal by the comparatively very much greater development of the left visceral ganglion (see also p. 7, fig. 3).

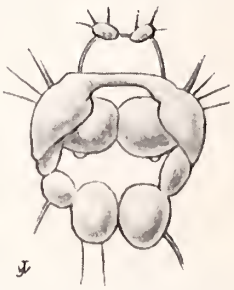


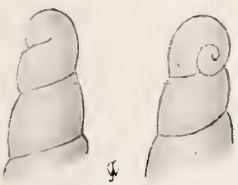
Fig. 257.—Nerve ring of *Limnæa peregra* (Müll.), showing the dextral character of the animal by the relatively greater development of the right visceral ganglion (see also p. 7, f. 3).

the osphradium—which is situate near the respiratory orifice on the left side, but this organ is placed dextrally in the *Limnæinæ* in correlation with the opposite arrangement of the organs of the animal.

The character of the organization is further indicated by the position of the heart, and the situation of the reproductive and other orifices, the latter being always upon the right side of the body in a dextral animal and upon the left side of a sinistral one. The heart, which is placed towards the periphery of the whorl in both dextral and sinistral shells, is on the contrary normally situate on the left side of a dextral animal, and on the right side of a sinistral one, but

does not invariably correctly indicate the organization, as it is always in proximity to and in close association with the respiratory organs, changing its position in correlation with the modifications which the breathing organs are so liable to undergo. In *Ancylus*, which is a hyperstrophic species, the respiratory cavity has been lost, and the function of respiration assumed by the left margin of the mantle and by a secondary pseudo-branchial appendage, which has been developed on the same side, the heart having moved in correlation with this development from its normally dextral position towards the left side, so as to retain its proximity to the functional aërating organs. The embryo of *Planorbis corneus* has a spirally sinistral shell, with the heart on the right side of the body, thus indicating a sinistral organization of the animal, but as growth proceeds the heart gradually moves dorsally and nearer the left side, probably in correlation with the development of an auxiliary branchia upon the left side, and the shell gradually becoming a discoidal and practically dextral species, and therefore heterostrophic in character.

Heterostrophic (ἕτερος, other [than usual way]; στροφή, a turn) shells are those which do not continue their growth in the same direction as they begun, but at a certain period of their existence gradually, but quickly, change that direction, so that a sinistrally organized species may commence life as an orthostrophically sinistral shell, and end as a hyperstrophically dextral one; or, on the contrary, may be at first hyperstrophic, that is, a sinistrally organized animal may have a dextrally coiled shell, which afterwards becomes sinistrally convoluted or orthostrophic and in accord with the organization of the mollusk, and *vice versâ*; yet the enrolment of all these forms always belongs to the same spiral, which may, as pointed out, be at first negative and afterwards become positive, or the reverse, the differently coiled embryonic portion being often left as though affixed to the side of the apex of the spire. In addition to the *Planorbes*, we have an example of these heterogyrate forms, as such shells are also called, in *Ancylus*



Figs. 258, 259.—Portion of spire of *Turbonilla rufa* Phil., showing how the change from hyperstrophically sinistral to orthostrophically dextral coiling takes place (after Fischer).

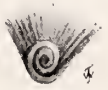


Fig. 260.—Apex of shell of *Ancylus fluviatilis* (Müll.), showing the orthostrophically sinistral coiling of early life, which later becomes hyperstrophically dextral in character (after Bourguignat).

fluviatilis, which, according to M. Bourguignat, is in its early stages sinistrally coiled, and only later tends to become a dextral shell, being apparently somewhat analogous in this respect with *Anastoma*, though coiled in the opposite direction.

A sinistral shell can be readily recognized by holding the shell with the aperture towards the observer and its apex pointed upwards, when, if dextral, the aperture will be on the observer's right, and, if sinistral, on his left; but this simple and easy test does not enable us to detect or recognize those shells which have been subjected to hyperstrophic development.

Scalariformity (*scalaris*, a flight of stairs; and *forma*, form) of the shell is the separation or dislocation of the whorls and is a phenomenon to which all spirally coiled shells are liable, possibly owing to some internal peculiarity of, or injury to, the organization of the animal, or, at least in some cases, to the adherence of extraneous matter to the immature shell or other cause interfering with the close apposition of one whorl with another, and in correlation with the amount of obstruction the obstacle offers to the normal growth, the degree of scalarity in the shell is dependent, as it usually follows for the rest of its growth the direction thus accidentally given to it. If the interference be comparatively slight and near the suture, a canaliculate suture may be formed, which may continue quite to the aperture, or may only exist for a limited distance, the growth becoming normal after passing beyond the obstruction.

Fig. 261.—*Helix aspersa* monst. *cornucopia* Gmelin,
Mawnan Sanctuary, near Falmouth,
Collected by the late Rev. W. Rogers,
An example of extreme scalarity.

Remarkable examples of extreme scalarity are furnished by the ceratoid specimens of *Helix aspersa* and other species.

The flatly-coiled or discoid shells of *Planorbis* are equally or even more liable to become spirally elevated with more or less regularity, as in *Planorbis marginatus* monst. *cochlea*, which may in that state be easily mistaken, at a casual glance, for *Valvata piscinalis*, to which species it bears a great resemblance.

Fig. 262.—*Planorbis marginatus* m. *cochlea* Brown × 3,
Risegate Eau, Gosberton,
Collected by Mr. H. Wallis Kew, F.Z.S.,
Showing a scalariform shell.

It was originally described in 1818 as a new species by Capt. Brown under the name of *Helix cochlea*, and Dr. Turton the following year described it as *Helix terebra*, but it was afterwards reduced from specific rank and the shell allocated to its appropriate species when its affinities were recognized. This dislocated spiral coiling seems to be more especially the result of the peculiar and abnormal conditions arising from living in waters modified by the warm water, and perhaps other substances, emanating from steam engines. A reservoir at Swansea, the water of which was kept at a high temperature by the influx of condensed steam, etc., from steam engines, was inhabited by *Planorbis marginatus*, and all the specimens tended to assume the raised spiral form. The mill-pond at Rochdale, which has been so often recorded for its plentiful production of this monstrosity, was subject to the same conditions as the reservoir at Swansea. The whorls may also become quite detached and separate like a *Vermetus* or a corkscrew, although the extreme openness of the spiral coiling is seldom so pronounced and regular as in the palæogenic specimen of *Planorbis spirorbis* I have figured. Sometimes, but more rarely, the whorls coil closely in a cylindrical fashion, like those of *Pupa*; I have only seen this deviation in *Planorbis marginatus* and *Planorbis vortex*. *Planorbis marginatus* seems especially liable to produce these scalarid monstrosities, but *Planorbis spirorbis* shows the most pronounced and decided tendency to revert to the original sinistral direction of coiling.

Fig. 263.–*Planorbis spirorbis* monst. *priscum* Taylor × 3, Pond, Hayling Island, Hants., Collected by Mr. H. H. Haines.

Fig. 264. — *Planorbis vortex* monst. *columella* Taylor × 3, Ditch, East Moors, Cardiff, Collected by Mr. F. W. Wotton.

One of the causes inducing this scalarity in the *Planorbes* has been conclusively demonstrated by Van den Broeck and others to be the thick and occasionally matted growth of *Lemna minor* covering the ponds inhabited by the *Planorbes*, and preventing the easy access of the discoidal shells to the surface for respiration, the young and the scalariform specimens being proved by experiment to penetrate the dense vegetation with far greater ease and celerity.

In the Lake of Magnée, in Belgium, where this deviation in *Planorbis marginatus* was found in great abundance, and the normal

discoid form but rarely, the surface of the pond was thickly covered by a very dense growth of the *Lemna*, but on the plant afterwards dying away, the scalarid specimens ceased to be produced, and the ordinary discoid shells only were to be found.

Herr Clessin records that the same deformities are produced in various species by ponds filled with other water plants, or on the shores of lakes among and between stones.

A further cause suggested is that, during the growth season, the water in the ditches or ponds inhabited by these species is often nearly dried up, and that the efforts of the creatures in forcing their way through the thick mud in which they are sometimes left partially imbedded, to again reach the water, may easily cause an alteration in the direction of the new growth, if at the time in process of formation.

M. Roffiaen endeavoured to produce scalariform specimens of *Helices*, at will, by attaching plaster-of-Paris upon the penultimate whorl, near the suture or line of attachment of one whorl with another, but he was in a degree unsuccessful in the attempt, as the mollusks, after surmounting the obstacle placed on their line of growth, reverted to their normal manner of coiling, or produced only irregularly grown and deformed shells, quite different from the symmetrically and gracefully coiled scalariform shells naturally produced. The result of the experiment led M. Roffiaen to believe that scalariformity in shells is owing to some accidental modification in the animal, such as the permanent contraction or relaxation of certain muscles could produce.

FIG. 265.—*Helix nemoralis* monst. *scalariforme* Taylor,
Ballyshannon, Donegal,
(Mr. W. Swanston's collection),
Showing a naturally grown scalariform shell.

FIG. 266.—*Helix aspersa* Müll.,
Reared by Mr. J. Madison,
Showing an artificially produced scalariform shell.

Mr. J. Madison has also endeavoured to produce these scalariform shells by similar means to those adopted by M. Roffiaen, and has been to a similar extent successful in inducing the desired scalarity, but hopes to have much more symmetrical and finer results as he gains more experience in their treatment.

Polystomatism (πολύς many, στόμα mouth) is a term denoting the presence of more than one aperture to a shell, and is most liable to occur amongst the individuals of those species with greatly contracted apertures, especially those forming the genus *Clausilia*, which are, under certain circumstances, liable to form an additional or second aperture. These dual-mouthed shells might possibly be regarded by novices as the joint production of two individuals united together, but with the head and neighbouring parts distinct and separate—a kind of Siamese twins—but this second aperture is probably formed on account of some obstacle or hard particle becoming fixed, temporarily or permanently, in the normal one, thereby deranging or obstructing the action of the clausium, and preventing the egress of the animal, which is therefore compelled to form a new outlet or perish confined within its shell. This new outlet is made by piercing the shell-wall, usually about half-a-whorl distant from the original one, and thus facing in the opposite direction, and is formed exactly in the normal way. Mr. P. B. Mason mentions specimens of *Clausilia* with as many as four distinct mouths to the shell.

Fig. 267.—*Clausilia bidentata* (Ström) × 2,
Luton, Bedfordshire,
Collected by Mr. J. Saunders,
Showing the two distinct mouths of the shell.

Although the wide-mouthed shells do not appear to be so liable to this peculiarity as the *Clausilia*, which have a very contracted and dentate aperture, yet I have a very interesting distomate specimen of *Limnæa auricularia*, kindly given me by Mr. H. Wallis Kew, and found by him at High Beach, Epping Forest, in 1894. This shell, from some inexplicable cause, has discontinued the use of the normal aperture, and pierced the outer shell-wall or perhaps availed itself of an accidental fracture of the body-whorl, about a quarter of a volution from the outer lip, and there constructed a new and more contracted opening which, despite its comparatively restricted size, appears to have been used as the means of exit. This new growth, forming the protruded new outlet, would appear to have been formed after the atrophy of the glands of the collar, as it is deficient of epidermis, and is apparently formed by the general surface of the mantle.

Fig. 268.—*Limnæa auricularia* (L.),
High Beach, Epping,
Collected by Mr. H. Wallis Kew, F.Z.S.,
Showing two distinct and separate apertures to the shell.

Polyperistomate (πολύς, many; περί, around; and στόμα, mouth) would perhaps be a more correct designation for certain shells, which though differing somewhat from the truly distomate shells, are yet equally interesting, and of which the *Limnæa peregra* discovered by Mr. William Nelson in the spring of 1883 in a small shallow cattle pond at Allerton-Bywater, near Leeds, are a remarkable illustration. These shells, and all in the pond were more or less affected, are somewhat irregularly and often fantastically grown, and in addition to this malformed growth, sometimes developed two or more complete peristomes or lips to their shells; these lips, though more or less confluent and grown together at the posterior margin of the shell, become quite distinct and separate at the anterior or basal portion, and the complete shells have in some cases all the appearance of one or more distinct shells enclosed within a larger external one.

Fig. 269.—*L. peregra* (Müll.) × 2, Pond, Allerton-Bywater, Yorks., Collected by Mr. W. Nelson, Showing three distinct and separate peristomes.

The Pelecypods also occasionally exhibit this duplication of the apertural margin, and characteristic specimens present, as in the

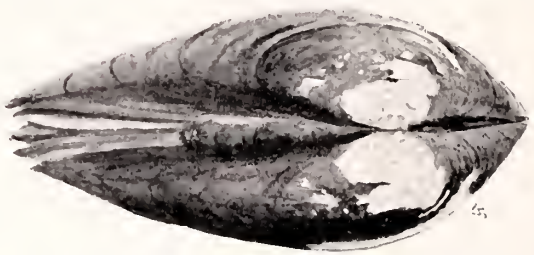


Fig. 270.—*Unio tumidus* Phil., Groby Pool, Leicestershire, collected by Mr. H. E. Quilter, Showing the formation of three distinct and successive peristomes.

Limnæa peregra above mentioned, all the appearance of several shells enclosed within an outer larger one, and in an even more deceptive manner.

These additional lips are usually of less amplitude at their origin than the one previously made, and have been noted to be often formed in spring, when the emaciation or reduction in bulk of the body which may be assumed to take place during hibernation has not been fully compensated for before the growth season has recommenced and this diminished size of the body would necessitate a contraction in the

size of the shell. Irregularity in food supply, due to the recurrence of alternating periods of enforced abstinence, owing to food scarcity, followed by terms during which ample supplies of nourishing and palatable food are easily obtainable, may be supposed to conduce to similar growths.

An Abnormal Continuation or prolongation of the regular growth is occasionally made after the normal completion of the shell and the formation of the lip, but in nearly all these cases, owing to the glands of the collar becoming atrophied at the maturity of the shell, these extraordinary and abnormal growths are exclusively secreted by the visceral mantle, and are therefore quite destitute of epidermis and of the middle calcareous layer with which the coloring matter is usually associated, having exactly the same character and appearance as the repairs made to damaged parts of the shell, remote from the aperture and beyond the reach of the collar; such repairs are made solely by the visceral mantle. These abnormal growths are probably only another mode in which the result of the prolonged life of the animal may be manifested, and in all likelihood this assumed protracted life's cycle of the mollusk is owing to unusual mildness of the seasons. The locality where the specimens figured and others also have been obtained is very suggestive, the neighbourhood being noted for its genial and mild climate.

Fig. 271.—*Clausilia bidentata* (Ström) × 2, Cheltenham, Collected by Mr. W. Nelson, Showing abnormal continuation of growth.

Fig. 272.—*Helix nemoralis* (L.), Cheltenham, Collected by Mr. W. Nelson, Showing abnormal continuation of growth.

In some rare instances it may happen that the aperture is formed prematurely, and normal growth be afterwards continued for a short distance, and a new apertural margin formed, or it may be that in some cases the atrophy of the glands of the collar may be delayed longer than is usually the case.

Anomalous Combination Shells are those formed by the union of two or more diverse shells, either owing to the circumstances producing them occurring naturally, or through artificially bringing the desired shells into the necessary close conjunction with each other, so that

the animal may permanently attach them together on continuing its growth. M. Barthelmy, director of the Marseilles Museum, once found a *Helix aspersa* which had evidently become lodged by some means within the empty shell of a *Limnæa stagnalis* before attaining its full growth, and which in its progress to maturity, attached its own shell by the new growth to the shell of the *Limnæa*.

FIGS. 273, 274.—*Helix aspersa* Müll., Collected by M. Barthelmy (after S. Petit), Showing the conjunction of two diverse shells.

Mr. Madison, of Birmingham, has been very successful in obtaining a number of these grotesque shells. Through his kindness I have had the opportunity of examining many of the results of his patience and ingenuity. Some of the *Helix aspersa*—with which species he has mainly experimented—he has induced to incorporate with their shells, in the process of their growth, full grown shells of *Helix cantiana* and other species in various odd positions; he has also contrived to join with the growing shell of the mollusk more or less complete nut-shells and other objects. His series of these curious monstrosities is interesting and remarkable.

FIG. 275.—*Helix aspersa* Müll., Reared by Mr. J. Madison, Showing a Barcelona nut incorporated with its shell by the mollusk.

In the Woodwardian Museum, Cambridge, there is a similar monstrous specimen from Ulverston, possibly naturally grown, in which two shells of *Helix aspersa* have grown together in this way.

M. Cailliaud has described the method of producing the union of these diverse shells to be by breaking away the palatal or outer margin of the shell of an *Helix aspersa*, or any other species that may be selected for the operation, and then introducing the living mollusk into the empty shell which it is desired should be incorporated with or joined to its own, attaching the two together for a few days only by the aid of thread or other suitable means, the mollusk usually in that time has cemented the two shells together by the new growth it has been stimulated to make by the removal of portions of its shell.

Auxiliary and Protective Organs.

There are three ingenious, though dissimilar methods, by which Univalves close the apertures of their shells, for the double purpose of protection against the intrusions of their enemies and to prevent the desiccation or evaporation of the natural moisture of the tissues of the body, during the mid-day periods of repose or the more extended dormancy of æstivation and hibernation, and also to guard against the extremes of cold, heat, and the injurious effects of climatal fluctuations generally.

These auxiliary organs, known as the Operculum, the Clausium, and the Epiphragm, are formed in an analogous way to the shell itself, the secretion to form these different organs being probably poured out as a gelatinous substance holding calcareous matter in solution, which hardens and crystallizes by exposure, the semi-fluid chitinous matter, which constitutes the investing and permeating organic framework, moulding itself around the growing crystals formed by the calcareous matter present in the solution.

The Operculum (*operio*, to cover) is perhaps the most important and universal of these contrivances for closing the mouth of the shell, and is a special structure chiefly developed amongst the branchiferous Gastropods, but has been retained in some genera which have probably become adapted to terrestrial life and aërial respiration.

It originates upon the embryo in the ovum, above the foot, and at the posterior end of the body, upon a restricted portion distinguished by its denser texture, which has been termed the operculigerous lobe, and presents, especially in genera foreign to our limits, very great diversity of structure, but our native operculiferous species are very few and do not exhibit the remarkable forms of many exotic species. It may consist of chitinous layers, as in *Vivipara contecta* and other species, but is sometimes strengthened by calcareous matter, as in *Neritina fluviatilis*, etc., the inner surface being always marked by a muscular scar showing the point of attachment to the animal and shell.

The operculum is usually, but not invariably, the size of the aperture it closes, and according to Mr. Kenneth McKean in *Bythinia tentaculata* fits the mouth of the shell so accurately that if the animal be killed with boiling water and allowed to dry up within the shell, and it be afterwards held in the warm hand, the operculum will fly off with a considerable report owing to the expansion of the confined air or gas.

The position of the operculum upon the animal varies within certain limits in the different species. In *Neritina*, when the animal is crawling the operculum practically hinges on the columella, but in other genera it may be at a comparatively considerable distance from the aperture. The operculum is brought over the mouth of the shell to close the aperture when the animal retires, by the contraction of the retractor muscle to which it is attached; the point of insertion usually leaves a single scar upon the operculum, but on that of *Neritina fluviatilis* there are two scars, that formed by the hinder muscle being the largest and forming a broad submarginal scar along the side adjacent to the columella, while the scar at the anterior end is smaller and is of a somewhat ovate shape and situate at the base of the opercular process, termed the "peg," which is, however, rudimentary in our British species, and therefore usually quite overlooked by most conchologists. The muscles are attached to the shell at opposite ends of the pillar lip.

Fig. 276. — Section through the shell of *Neritina fluviatilis*, showing the operculum *in situ* and the mode in which the "rib" hinges upon the columella, × 3 (section cut by Mr. F. Rhodes).

The operculum varies even more than the shell in the relative amounts of chitinous and calcareous matter contained in its composition. In some species, as *Neritina fluviatilis*, the operculum has comparatively less organic and more calcareous substances than the shell whose mouth it closes, while that of *Vivipara vivipara* is purely chitinous, the gravimetric tests made upon clean opercula by Mr. Crowther showing no trace of lime, although the shell of that species contained 94·24 per cent of earthy salts.

The composition of the operculum of *Neritina fluviatilis* has been termed "not shelly" by some authors, and purely calcareous by others, but a careful analysis showed it to contain 97·32 per cent of inorganic matter and 2·67 per cent. of organic substances; the shell of the same species however contains more organic matter than its operculum having 4·40 per cent. of organic substances and only 95·59 per cent. of inorganic matter in its composition. The organic skeleton of the operculum of this species is not destroyed even by mixed acids, the chitinous framework preserving its form and elasticity unimpaired and making a pretty object under a lens.

Cyclostoma elegans, on the contrary, has less chitinous matter in the shell than in its operculum, the analysis showing the operculum to contain 92·76 per cent. of inorganic matters and 7·23 per cent. of

organic or chitinous substances, the shell having 98·94 per cent. of inorganic and 1·05 per cent. of organic matters.

These analyses of shells and opercula made for me by Mr. Crowther, still further demonstrate that the composition of the calcareous parts of the shell and operculum are not strictly identical in character, as the calcareous matter of the shells rapidly dissolved and disappeared upon immersion in hydrochloric acid, while the calcic constituents of the opercula were very difficult to dissolve, even in warm acid.

It has been suggested by Adanson, Gray, and others, that the shell and its operculum were together homologous with and represented the two valves of the Bivalve, but Huxley considered the operculum to be the analogue, if not the homologue, of the byssus of the Bivalve, and that it cannot represent the valve of the shell, which is a pallial structure; there is, however, a somewhat striking analogy between them, as the operculum is attached to the shell itself through the body of the animal by a powerful muscle corresponding to the posterior adductor of the Lamellibranchs, which it may be also considered to represent in function. Another remarkable peculiarity possessed in common, is that when the mouth of the shell is closed by a spirally coiled operculum the spiral always revolves in the opposite direction to the spire of the shell, a dextral shell having a sinistral operculum and *vice versâ*, exactly as is the case with the two shells of a Bivalve, the right valve of which may be twisted or coiled at the umbo to the right, in which case the left valve would be coiled or turned to the left. In those species like *Neritina fluviatilis*, the similarity is still further marked by the development of complex calcareous processes on the inner side of the operculum close to the columella, which have been designated as the "rib" and "peg," the rib functioning similarly to the interlocking teeth in bivalves, and even in species with a lamellate or concentric operculum, the nucleus or representative of the umbo is always nearest to the columella, or what would be the hinge line. The different forms of opercula are characterized as

Spiral when spirally formed; the coiling is sinistral in dextral shells and dextral in those sinistrally coiled, and the increase is derived from a portion only of the operculigerous lobe, exactly as the increase in size of shells is due to the mantle margin. The spirally coiled opercula actually revolve or turn upon the columellar muscle during the progress of growth, as is shown

by the fact that the termination of the spiral where the enlargement is exclusively made always abuts against a certain definite part of the aperture of the shell, and thus clearly establishes that the operculum must of necessity, in the course of growth, actually revolve upon the end of the columellar muscle as many times as there are whorls or coils indicated thereon. These spiral opercula may be distinguished as

Paucispiral, or few whorled, the nucleus being placed towards the basal or anterior end, as in *Cyclostoma elegans*, *Acicula lineata*, etc. The operculum of *Cyclostoma elegans* is chiefly and very distinctly formed of two thin laminæ, as its channelled edge clearly indicates; or

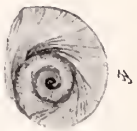


Fig. 278.—A Paucispiral Operculum × 3.
Cyclostoma elegans (Müll.), Box Hill, Surrey, Collected by Mr. W. Whitwell, F.L.S.

Multispiral, or many whorled, the nucleus being situate towards the centre of the organ, as in *Valvata piscinalis*, but the number of whorls in the operculum has no necessary relation to the number in the shell, though at times in accord with it. Dr. Jeffreys describes and figures the operculum of *Valvata piscinalis* as formed of 10 to 12 spiral whorls, and Moquin-Tandon figures the same as containing only 4½ volutions, though describing it correctly in the text.

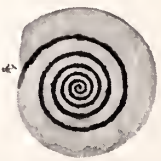


Fig. 279.—A Multispirally-coiled Operculum × 8.
Valvata piscinalis (Müll.), River Tarff, Kirkcudbright, Collected by Mr. F. R. Coles.

Concentric when the increase in size takes place from the whole surface of the lobe, and more or less equally around the sub-central nucleus; such opercula do not alter their position upon the retractor muscle to which they are affixed, but accommodate themselves by simple growth to fit the increased size of the aperture of the shell, as in *Vivipara contecta*, etc.

Fig. 277.—A Concentric Operculum × 1½.
Vivipara contecta Millet, Southport, Collected by Mr. G. W. Chaster.

Articulated when furnished with more or less complex projections or apophyses, which appear to act like a hinge, as in *Neritina fluviatilis*. The operculum of this species has a broad flexible margin, and is duplex in character, being distinctly and marginally subspiral on the external face, but this feature is practically obscured on the internal face by a later calcic deposit.

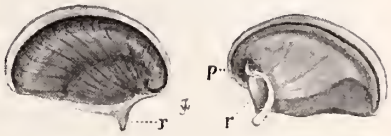


Fig. 280. Fig. 281.
An Articulated and Sub-spiral Operculum × 4.
Neritina fluviatilis (L.),
Canal, Northampton,
Collected by Mr. W. D. Crick, F.G.S.,
Fig. 280 showing the external face and the subspiral formation of the operculum, with the projecting "rib," and Fig. 281 showing the interior face with sub-marginal muscular scar, the "rib" and "peg," and anterior scar, at base of the apophyses.
r. rib or fulcrum ; *p*. rudimentary peg.

The different parts of the operculum may be distinguished according to its position when applied to the mouth of the shell, the Exterior face being that facing outwardly and the Internal face that to which the columellar muscle is attached; the part adjoining the base of the aperture of the shell may likewise be termed the base or Anterior end of the operculum, the opposite end being the upper or Posterior one, the Palatal margin of the operculum is the one adjacent to the palatal or outer lip of the shell, and the Columellar side the one adjoining the columellar margin.

The Clausilium, or Clausium (*clausum*, an enclosure), as I prefer to call it, is another ingenious contrivance, formed within the last whorls of the shell in the genus *Clausilia*, also for the purpose of closing the aperture against outside enemies and preventing desiccation. It is an elongate, somewhat oval, externally convex, and more or less arcuate, nacreous-white plate or lamella, attached by a somewhat cartilaginous, elastic and spirally twisted pedicle or footstalk to the columella near the commencement of the penultimate whorl, and has been aptly compared to a door furnished with an elastic spring. It also varies greatly in its form and character in the different species and in correlation with

Fig. 282.—Clausium of *Clausilia bidentata* Ström × 8,
Stroud, Gloucestershire,
Collected by Mr. E. J. Elliott,
Showing the convex external face of the clausium and its elastic pedicle of attachment.

Fig. 283.—Clausium of *Clausilia cravenensis* Taylor × 8,
Starbotton, Yorks.,
Collected by Mr. W. D. Roebuck,
Showing the convex external face of the clausium and its elastic pedicle, for comparison with that of *Clausilia bidentata* (fig. 282).

the palatal plications that may be present in the shell, exhibits a corresponding and appropriate situation of its external outline, and is an organ certainly deserving of much more careful study than it has hitherto received from British conchologists.

Fig. 284.—Clausium of *Clausilia laminata* (Mont.) × 8.
Cooper's Hill, Cheltenham,
Showing the concave internal face and the sinuate lower margin.

Unlike the operculum, which is attached to the animal and present from the earliest age, the clausium is attached to the shell only, and is not present in the young, being only produced at the approach of maturity, the pedicle being first formed and the lamella gradually added to until completed.

When the animal emerges from the shell, the clausium is pushed by the pressure of the body against the columella, into the groove between the inferior and subcolumellar lamellæ, thus leaving the means of exit free. On the withdrawal of the animal into the shell the pressure of the body against the lamella is removed and the elastic pedicle causes the filament to spring into its normal position, with its lower margin against the exterior of the whorl, but when the shell is thus closed there still exists a small opening near the suture which is conjectured to serve for respiration and defecation. In the empty shell from which the animal inhabitant has been removed and the lamella become rigid and dry, the elasticity can be to some extent restored by immersion in water.

Fig. 285.—Section through shell of *Clausilia bidentata* Ström, showing the clausium *in situ*, × 4 (section cut by Mr. F. Rhodes).

Fig. 286.—*Azeca tridens* (Pult.) × 6.
Roundhay, near Leeds,
Showing the inflexible calcareous lamella, assumed to represent the Clausium.

Though especially indicative of the *Clausiliæ*, there is found in *Azeca tridens* an imperfect, rudimentary and inflexible lamella, which is attached along its whole length to the columella, and has been assumed to represent the more elastic clausium. This rigid calcareous fold is continued quite to the aperture of the shell, within which its rounded termination may be seen parallel with the columellar margin.

Daubenton was the first to notice this remarkable appendage, but Müller gave the first full and accurate account of its function and structure under the names of Ossicula and Scala. Draparnaud in 1801 and Miller in 1822 independently discovered and described it, apparently in ignorance of the work of their predecessors.

The Epiphragm (ἐπί, upon; φράγμα, protection) or Hybernaculum, as it is sometimes called, is another means of protection to the animal when enclosed in the shell, though differing essentially from both the operculum and the clausium, as the former is permanently attached to the animal and the latter permanently fixed to the shell, while the epiphragm has no organic connection with either the shell or animal. The epiphragm presents neither appendages nor incremental marks, as in the clausium and operculum, and is only temporarily adherent to the shell, from which it is cast off and renewed as often as the animal's necessities require.

According to Binney, when the mollusk desires to form an epiphragm, it withdraws within its shell, and brings the collar of the mantle to near the level of the aperture, exuding therefrom a quantity of mucus, more or less intermingled with calcareous particles, sufficient to cover the exposed surface; the mucous pellicle is then detached from its adherence to the animal by a small quantity of air emitted from the respiratory orifice, which projects the film into a convex bubble-like form, the animal at the same moment shrinking further within the shell, and the external air forcing the delicate epiphragm to a flat or even concave shape; it then hardens and becomes fixed to the inner margin of the aperture of the shell. All these actions are almost instantaneously effected by the animal.

The epiphragm is composed of the mucoid secretions of the animal, mingled with calcareous granules, some of which exhibit a concentric structure; it is permeable to air and not softened by or soluble in water and varies very greatly in character not only according to the species, but even in the same individual, according as to whether it is secreted for protection during the winter dormancy or merely to prevent the drying of the tissues during diurnal repose or enforced abstinence. The diurnal or summer epiphragm is,

Fig. 287.—*Helix nemoralis* L. Castle Hill, Scarborough, Showing *in situ* the thin, iridescent diurnal or summer epiphragm, with the white calcareous thickening in front of the respiratory orifice.

in this country, much more delicate and less intermingled with calcareous particles than that formed for winter protection, being often of exceeding tenuity and transparency and beautifully iridescent. There is an opaque and usually very apparent white calcareous spot opposite the orifice of the respiratory chamber, through which there often passes an opening or slit in the film, which though not invariable in its direction, is usually parallel with the outer margin of the shell.

The point where the animal was last in contact is often somewhat puckered and irregular, and, like the circumscribed area opposite the respiratory orifice, has a whiter and more opaque character, owing to a greater density of the calcareous matter at that place. Additional layers may be afterwards added which strengthen and thicken the film.

Fig. 288.—*Helix pomatia* L., Faversham, Kent, Collected by the late Miss E. B. Fairbrass, Showing the strongly calcareous winter epiphragm *in situ*.

The winter or hibernal epiphragm is always thicker and more solid than the ordinary one. In *Helix pomatia* it is very thick, strong, and calcareous, with an outward convexity, which seems to distinguish those species with bulky bodies. Animals with more meagre proportions relatively to their shell often have the epiphragm deeply sunk in the aperture. Species with a less calcareous shell and those destitute of a submarginal rib to the aperture have very thin, delicate, and often more or less imperfect ones, and all intermediate stages exist.

If the weather becomes very severe the animal shrinks further and further into the recesses of the shell, forming additional epiphragms at short intervals from each other, these becoming more and more delicate and transparent and less and less mixed with calcareous matter. I have myself counted as many as six of these septa in a Yorkshire specimen of *Helix aspersa*.

Some authors state that the epiphragm is only partially formed if the aperture of the shell is already partly closed by adherence to the shell of another mollusk or any other object, the epiphragm in that case being said to be secreted merely to close up the space not occupied by the object to which the mollusk is attached. I have, however, frequently verified in *Helix aspersa* that the epiphragm is complete and extends over the whole aperture, and is not invariably the partial production it has been asserted to be.

According to M. Delacroix the epiphragm of *Helix pomatia* contains nearly three times more animal or organic matter than the shell, his analysis furnishing 57·20 per cent. of organic matter, 28·03 per cent. of carbonate of lime, and 14·77 per cent. of other and undetermined mineral substances. Mr. Crowther, who has analysed an epiphragm of the same species from Faversham, found it to contain 6·83 per cent. of organic matter and 93·16 per cent. of inorganic substances. This analysis though differing so markedly quantitatively from that of M. Delacroix agrees in showing the epiphragm of this species to contain considerably more organic matter than the shell.

Though the formation of an epiphragm is more especially a characteristic of the inoperculate land shells, yet many freshwater species in times of drought, when the streams and pools they inhabit become dried up, not only bury themselves more or less deeply in the mud, but some species of *Planorbis* close the aperture of the shell by a strongly-adherent, firm, whitish epiphragm. *Planorbis spirorbis* is most addicted to the exercise of this power, and one of its synonyms, *Planorbis leucostoma*, probably indicates its habitual indulgence in this habit, though other species have also been observed in the same condition.

Those terrestrial species destitute of a sufficiently capacious external shell, within which they can retire for protection during unusually cold or dry weather, excavate for themselves a subterranean chamber, the walls of which are rendered smooth, coherent and firm by an internal coating or lining of the mucous exudations of the animal. This mucus-lined earth chamber, within which the creature lies snugly ensconced in a contracted and torpid state, may be considered as a peculiar and interesting modification of the apertural epiphragm of the testaceous species.

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The Animal.

The mollusks or animals, forming the shells described in the foregoing pages, have soft, unsegmented, and more or less bilaterally symmetrical bodies, whose external morphological features have been greatly changed by the excessive development in size and modification in form of particular organs, or by their diminution or even total suppression and loss in mature life. The foot, the mantle, and the ctenidia or branchiæ have perhaps undergone the most remarkable changes, although the foot or podium has been considered to be the most permanent and distinctive molluscan organ, and its modifications very appropriately used as the basis for forming the great divisions or classes into which the mollusca have been primarily separated. This enlargement or atrophy, as the case may be, of the different organs of the body has caused a remarkably diverse and varied aspect in the different forms, but these modifications are always correlated with and dependent upon the changes in and elaboration of their various and respective functions.

Notwithstanding the great divergence in external shape brought about by these modifications, the internal organization in the different genera presents a rather striking uniformity in many points, and agree in possessing in common a number of structural characteristics not found in other groups of animals. Being without an external or internal locomotory skeleton, the mollusca would seem to be more especially adapted for an aquatic life, the locomotion of the terrestrial forms being limited and slow, although the different genera may be adapted to live under almost every variety of terrestrial and aquatic conditions, and are capable of swimming, floating, burrowing, crawling and even spinning mucous filaments to facilitate locomotion when occasion requires their use. Some species or groups

are highly predacious, others purely phytophagous, but the majority of our forms are quite omnivorous and devour almost any substances that come in their way.

EXTERNALLY the whole surface of the animal is formed by a layer of somewhat firm and elastic muscular tissue, overspread by cylindrical epithelial cells, which are often ciliated, more especially in the aquatic species, and in those parts not habitually concealed by the protecting shell; the ciliated areas in the terrestrial forms being more restricted in extent. Scattered over the whole external surface, but more densely aggregated in certain definite parts are a number of neuro-epithelial cells forming the terminations of the organs of general and special sensibility in the mollusk. Intermingled with them are the outlets of numerous unicellular glands which secrete the more or less viscous mucosity which renders the teguments supple and moist.

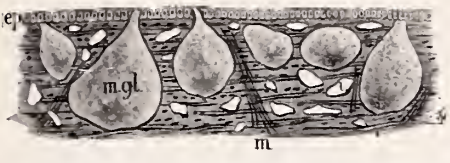


FIG. 289.—Section through skin of *Helix pomatia* showing epithelial and subepithelial structure, highly magnified (after Vogt aud Yung). *ep.* epithelium; *l.* small blood lacunæ; *m.* muscle-fibres; *m. gl.* mucus glands.

FIG. 290.—Neuro-epithelial cell of *Arion ater*, highly magnified (after Boll).

The body of the animal may be conveniently divided for study into four chief areas or regions, viz.:—The Cephalic, the Pedal, the Pallial, and the Visceral.

The CEPHALIC or Oral region is the anterior portion of the body, and bears the mouth or oral aperture and most of the organs of special sensibility, with appendages of various kinds.

The PEDAL or Ventral region is typically a well developed abdominal protuberance of variable shape, formed by a differentiation and thickening of the cutaneous and muscular tissue of that region, and constitutes the locomotor organ or foot. It varies in structure, size and importance in correlation with the active or sedentary habits of the animal.

The PALLIAL or Dorsal region is formed by a vascular expansion or duplication of the integument, called the mantle or shield, which partially or completely covers the more delicate parts or organs and hangs down around the body, the intervening space or cavity between the mantle and the body being known as the pallial chamber,

and primitively and usually contains the respiratory organs, and the various organic apertures, its thickened glandular margin secreting the calcareous and chitinous deposits forming the shell, although the shell-secreting function is not confined to this part, as the whole surface of the mantle is directly concerned in the formation of the internal calcareous layers of the shell, the animal being attached thereto by powerful muscular bands, which are symmetrically paired or unique according to the group ; and finally

The Body or Visceral region, which is generally developed in a more or less protuberant form and placed above the foot and partially or completely covered or enclosed by the pallium. It contains the organs of reproduction, the heart or motive centre of the vascular system, the alimentary canal, and various secretory and excretory organs.

Internally the general unity and agreement of the plan of organization, though it may have become more or less obscured by later developments and modifications, is much more evident.

Beneath the epithelium, the name given to tissue covering a free space, connective tissue of mesodermic origin is found, composed chiefly of vesicular and plasm cells, so closely interwoven with the subcutaneous musculature as to form a kind of dermo-muscular tube, to which greater firmness and rigidity is sometimes imparted by numerous calcareous concretions, produced by, and lodged within, its vesicular cellules. This interlaced subcutaneous stratum, sometimes called the corium, at times attains a great development, and gives rise to outgrowths of various kinds, which are liable to undergo concrescence or fusion amongst themselves, or with other organs of the body. The cœlomic cavity contains the various organs of the body and a great development of connective tissue, which is permeated in all directions by numerous hæmatocœles or blood-spaces, the distension of which by the circulatory fluid is the cause of the turgescence or enlargement of the different organs. This tissue originates in the form of polyhedral nucleated cells of homogeneous

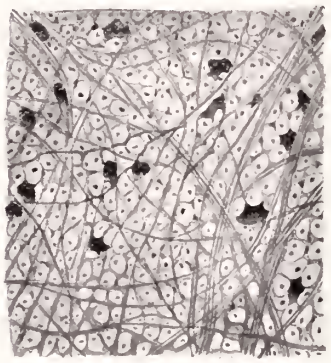


Fig. 291.—Typical Connective Tissue, rich in plasm cells and showing interlacing fibrillar bundles and small blood lacunæ, from *Helix nemoralis*, highly magnified (after Brock).

protoplasm, which with age acquire a fusiform, stellate or rounded form, but vary in aspect in the different regions of the body, and may become firmer, more compact and rigid, and constitute skeletal tissue, which surrounds or is distributed amongst the muscular and epithelial tissues, imparting consistency and strength, and constituting the supporting framework of the various organs.

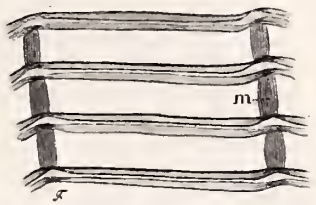


FIG. 292.—Chitinous and connective tissue framework of the outer ctenidium of *Anodonta anatina*, as example of skeletal tissue. *m.* transverse muscular fibres (after Vogt and Yung).

The organs of the body may be broadly classified according to their function and structure under six chief heads or systems, viz. :—The Nervous or Sensitive, the Alimentary or Nutritive, the Circulatory or Vascular, the Secretory or Glandular, the Muscular or Motor, and the Sexual or Reproductive systems.

The NERVOUS system, upon which all perceptive sensation depends, is concentrated in paired ganglionic masses in correlation with the bilateral arrangement of many of the organs of the body, and may be considered to be composed typically of four groups of more or less distinctly paired nervous masses or ganglia, viz. :—The Cerebral, the Pedal, the Visceral or Parieto-splanchnic, and the Buccal or Stomato-gastric. The Cerebral ganglia, which are placed above the œsophagus and innervate the head and its organs, are chiefly sensory in function; the Pedal, which are subœsophageal in position and innervate the foot, are more especially motor; while the Parieto-splanchnic and the Stomato-gastric centres, which are also situate or connected beneath the alimentary canal, and innervate the viscera, are to a certain extent analogous in function with the sympathetic system in mammals.

These various ganglia or nerve centres are constituted by a superficial or external layer of ganglion cells, which, according to Solbrig, have no proper membrane and are chiefly unipolar, with long, branching fibrillar extensions or processes, whose aggregation forms the central part or nucleus of each ganglion, and also pass into the nervous cords by which the various ganglia are connected together. Great variation exists in the degree of approximation of the different ganglionic masses; sometimes by specialization they become fused together and form a nerve-ring around the œsophagus, while in other groups the constituent ganglia may be variously combined together or widely

separated and distant. The nerves arising from these various centres innervate all parts of the body and take on definite duties or functions; those proceeding to the muscles are chiefly efferent or motor, while those terminating in sensory organs, whether merely tactile or of a more specialized character, are termed afferent or sensory.

Fig. 293. Fig. 294. Fig. 295.

Ganglion cells of *Unio pictorum*, highly magnified (after Rawitz). Fig. 293 from cerebral ganglion; Fig. 294 from visceral ganglion; Fig. 295 from pedal ganglion.

The various organs of special sense are nervous differentiations adapted to the various forms of perception suitable to the environment and habits of the organism, but the whole surface of the body is more or less acutely sensible to tactile and other impressions, although perception is more especially concentrated in the exposed and prominent portions of the body. The Auditory or Equilibrating organs are present in the active forms and are always buried in the tissues of the foot, though innervated by the cephalic ganglia, and consist of a pair of closed sacs, termed otocysts, lined with ciliated sensorial epithelium and enclosing calcareous concretions. The Cephalic Eyes are pigmented invaginations of the integument, usually closed by a layer of epithelium and containing a crystalline lens, and receiving their innervation from the cephalic ganglia. The skin generally is however dermatoptic and in a measure sensible to the influence of light and shade. The Olfactory organs are apparently influenced in their position by the character of the respiratory organs, as they may be located in the cephalic or in the pallial region, or be recognizably present in both areas; they are formed by the development and local concentration of neuro-epithelial cells, and according to their pallial or cephalic position may be innervated by the visceral or by the supra-œsophageal ganglia.

The Alimentary system by which nutrition is effected is a more or less complicated and diversified tube, composed chiefly of epithelial tissue, and embraces an anterior aperture or mouth, guarded by external lobes or palps, which leads by the œsophagus into a stomach or crop, into or near to which the usually voluminous liver or digestive gland discharges its secretion by suitable ducts. Occasionally the stomach has a cæcal diverticulum, within which, or in the intestine itself, there is a rod of gelatinous consistency, the Crystalline Style,

which is considered to be a secretion of the epithelium of the intestinal tract. The intestines are always considerably longer than the body cavity containing them, and are therefore necessarily thrown into a number of coils or convolutions, chiefly amongst the lobules of the liver, the absorptive surface being often greatly increased by a longitudinal infolding of its surface, called the typhlosole.

The CIRCULATORY system occupies the closed space or cavity between the alimentary canal and the external integument, and is formed by definite vessels in conjunction with a complex system of irregular spaces or lacunæ, which permeate amongst the various organs and within the interspaces excavated among the viscera, the muscular and connective tissue.

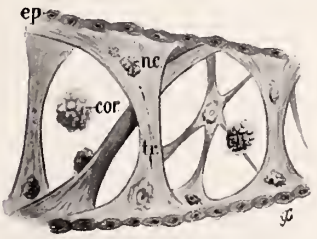


FIG. 296.—A fragment of subfilamentar lacunar or primitive mesoblastic tissue in *Anodonta*, showing the trabeculæ and their nuclei (after Holman Peck). *cor.* amœboid blood corpuscle, *ep.* epithelium, *nc.* nucleus surrounded by granular protoplasm, *tr.* trabecula showing peripheral expansion.

A dorsally placed heart or central motor of circulation is always present enclosed within a special chamber or pericardium, and is always arterial or systemic, the auricles receiving oxygenated blood from the respiratory organs and propelling it by means of a muscular ventricle through the body system.

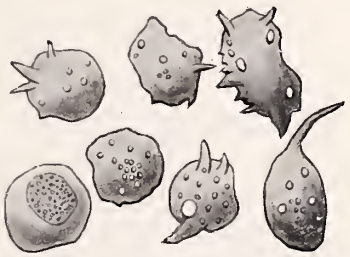


FIG. 297.— Amœboid blood corpuscles of *Helix pomatia*, highly magnified (after Vogt and Yung).

The blood or hæmolymph, which forms a large proportion of the total weight of the body, is usually a colourless or slightly opalescent albuminous fluid, containing numerous nucleated amœboid corpuscles, which are shed from the walls of the cœlomic space.

By far the greater number of mollusca in general respire by means of branchiæ or gills, and a few like *Planorbis* combine branchial and pulmonary respiration, but species with solely aërial respiration are confined to the Gastropoda. Respiration, however, is not confined to special organs, but is participated in by the general integument and more especially by the surface of the mantle, which is of a very vascular character.

The Glandular or Secretory system is a very important one, not only for preserving the external integument in a moist and supple condition by a plentiful secretion of mucus from the innumerable unicellular goblet-shaped glands scattered beneath and amongst the epithelium, but for the elaboration of the various ferments and secretions necessary for digestion and for the separation and elimination of noxious substances from the body. The Liver or Digestive Gland is one of the largest and most important organs of the body, and has probably a complex function, serving not only as a store-house for combustible fatty carbohydrates and a centre for secreting digestive ferments, but also contains numerous lime-secreting cells, whose products are said to be utilized in the formation of the shell and epiphragm. The Renal organs or Nephridia, which are in close association and connection with the pericardium, are very glandular in structure, and secrete or eliminate from the blood the waste products of the body in the form of urea or uric acid. The Pericardial Gland is also an excretory organ eliminating a still more acrid secretion, and, like the renal organs, is richly irrigated by the blood system, which circulates within the organ before entering the auricle.

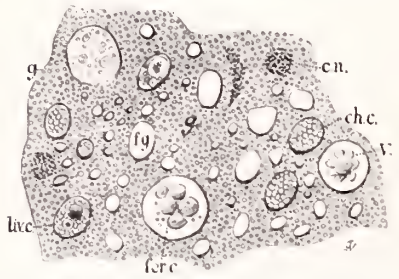


Fig. 298.—Elements of liver or digestive gland of *Helix pomatia*, showing its complex structure, highly magnified (after Vogt and Yung). *ch. c.* lime cells; *c. n.* cell nuclei; *f. g.* fat globules; *fer. c.* ferment cells; *g.* granular substance; *liv. c.* liver cells; *v.* vacuolated ferment cells.

Calcareous, Chitinous, and Pigmentary subepithelial cells of connective tissue are also placed in different parts of the body, but are more especially congregated at the thickened edge of the mantle, where they contribute to the formation and colouring of the shell.

The Muscular system is influenced greatly in its character and degree of development by the presence or absence of an external shell; its tissue is generally formed by smooth, cellular and unstriated band-like fibres, but those muscles capable of rapid contraction afford indications of their greater differentiation by displaying a deceptive appearance of striation sometimes arising from transverse rows of granules perpendicular to the axis of the fibre. The muscular

Fig. 299.—Unstriated muscle-fibre from foot of *Neritina fluviatilis*, highly magnified (after Boll).

system is developed in two chief layers : the Somatic and the Splanchnic, which are separated by the cœlomic or blood space, and are therefore practically independent muscular tubes, the somatic layer forming the external tube or body wall, and the splanchnic the internal tube or alimentary layer. The somatic, which is subjacent to, or beneath the external epithelium and more or less interlaced with the connective tissue, is usually the most developed, and, in addition to the transverse or annular fibres, has more deeply seated longitudinal ones, while radiate and oblique fibres are also present. The splanchnic layer which chiefly surrounds the alimentary canal is more delicate, but exhibits the same arrangement of annular and longitudinal muscular bundles as the somatic layer.

Fig. 300. — Pseudo-striate muscle fibre from buccal bulb of *Neritina fluviatilis*, highly magnified (after Boll).

This muscular tissue may become of a firmer and denser texture and show fibrous, membranous, or cartilaginous structure, and form the powerful muscular bands by which the animals are attached to and withdrawn within their protecting shell.

Reproduction in mollusca is not accomplished by any of the asexual methods which sometimes obtain in other lowly organized animals, but is always the result of the complete activity of both the male and female organs. The gonads or genital glands are usually more or less imbedded within the liver or digestive gland, the sexual elements, the spermatozoon and the ovum, being developed from the epithelial walls of the constituent cæca.

The generative organs are developed in two chief types—the Diœcious or bisexual and the Monœcious or hermaphrodite type—the diœcious type having the two sexes in different individuals and often exhibiting a noticeable sexual dimorphism in shell and animal, while in the monœcious or hermaphrodite type both sexes are combined in the same animal by a superposition of the male upon the female system. The prevalence of Proterandry or maturation of the male element before that of the female tends to prevent the possibility of self-fertilization, which, however, has occasionally been known to occur.

The reproductive system in mollusca is typically and primitively diœcious, which is a simpler arrangement than the monœcious or hermaphrodite condition, which usually exhibits several specialized

accessory organs, and is a later and more complex development, apparently influenced by the adoption of terrestrial or fluviatile life, parasitism, fixed habits, etc.

The Hypothetical Primitive mollusk, from which all the varied forms now existing have been derived, has been assumed, with great probability, to have been a bilaterally symmetrical animal, which possessed in addition to other general characters a well marked locomotor foot or muscular creeping disc and a more or less well-defined head, bearing a ventral mouth and paired tactile processes or tentacles, at the base of which were probably pigmented eye spots. Dorsally the animal was overspread by a fold of the integument, called the mantle, which hung loose at the margins around the body, forming a space or cavity between its free pendulous margin and the body-wall—the pallial cavity, within which were the paired feather-like gills and the excretory outlets. This integument had the physiological power of secreting a more or less calcareous shell, with a chitinous framework to which the retractor muscles of the body were firmly attached.

Fig. 301.—Hypothetical Primitive Mollusk, showing externally the dorsal shell, paired tentacles and over-hanging mantle margin and internally the alimentary canal, heart, branchia and genital glands, with longitudinal untwisted nerve cords and ganglionic enlargements (after Pelseneer).

The nervous system exhibited the archaic character of long paired nerve cords, with ganglionic enlargements on each side of the median line, arising from the paired supra-œsophageal ganglia and connected together beneath the alimentary canal or digestive tract, upon the course of which various ferment glands are developed. The auditory capsules or otocysts are placed in the anterior part of the foot, but innervated by the cephalic ganglia. The olfactory organs are sensiferous areas near the base of each branchia, which receive their nerve supply from the pallial ganglia. The gonads or genital glands are present as dependencies of the pericardial chamber, their products reaching the exterior by the reno-pericardial orifices.

The circulatory organs were confined within the secondary cœlomic cavity or pericardium, the heart however being probably primitively double, as suggested by Dall for the Protopelecypod, with a ventricle and an auricle on each side, the ventricles eventually fusing in the median line and, in some groups, enclosing the rectum.

From this archetypal form our various species have been evolved in the two well-marked divergent lines, Gastropoda and Pelecypoda, characterized by and receiving their names from the modifications the foot has undergone.

The GASTROPODA, pursuing an active and more or less aggressive mode of existence, have developed the most varied and numerous forms and are the only group of mollusks containing species organized for the respiration of free air; they have also retained and variously developed the sole-shaped locomotor foot and the distinct head of

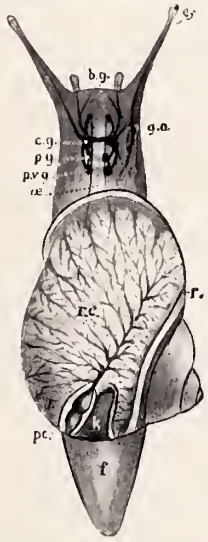


FIG. 302.

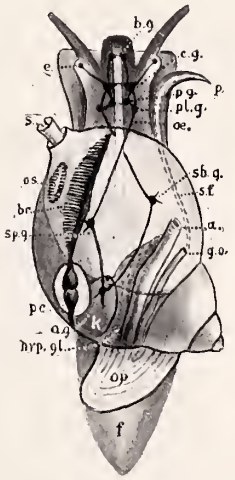


FIG. 303.

Fig. 302.—Schematic figure showing the arrangement of the internal organs in *Helix aspersa* as typifying the Euthyneura. Fig. 303.—Schematic figure showing the arrangement of the internal organs in the Azygobranchiate Streptoneura (after Lang).

a.g. abdominal ganglion ; *b.g.* buccal ganglia ; *c.g.* cerebral ganglia ; *p.g.* pedal ganglia : *pl.g.* pleural ganglia ; *p.v.g.* pallio-visceral ganglia, representing the long twisted nerve cords and ganglia of the Streptoneures ; *sb.g.* subintestinal ganglion ; *sp.g.* supraintestinal ganglion ; *e.* eye ; *os.* osphradium ; *a.* anus ; *œ.* œsophagus ; *k.* kidney or nephridium ; *r.* rectum ; *g.o.* genital orifice ; *p.* male organ ; *s.f.* seminal furrow ; *br.* branchia ; *pc.* pericardium, enclosing the heart ; *s.* siphon ; *r.c.* lung chamber, showing blood plexus ; *f.* foot ; *hyp.gl.* hypobranchial gland ; *op.* operculum.

their assumed ancestor, and acquired or elaborated a very remarkable prehensile and aggressive oral mechanism adapted for the seizure and comminution of food, but owing to the unequal pressure or strain upon the body, caused by the development of an univalve shell, they have lost the bilateral arrangement of many of their internal organs.

The various species have not however developed *pari passu*, and in accordance with the differences now exhibited are distinguished as Streptoneura and Euthyneura, the former characterized by the per-

sistence of the torsion of the visceral commissures, and secondarily by the less complete degeneration in the group generally of the primitively left organs of the pallial complex : and the Euthyneures, which have untwisted nerve cords and a greater concentration of the visceral nerve centres, with a more complete atrophy of the organs of the originally left side, perhaps due to the partial detorsion which the visceral sac has probably undergone.

Helix aspersa or *H. pomatia*, which may be accepted as representative of the Gastropoda, has a bilaterally symmetrical external aspect, with a compact but elongate body, covered with an external cuticle composed of distinctly nucleated epithelial cells, distinctly ciliated on certain portions of the body, and usually more or less darkly pigmented and tuberculate, but most strongly so in the anterior and dorsal regions, the pigmentation and rugæ becoming less pronounced and striking as the foot or the mantle are approached.

Fig. 301.—*Helix aspersa* Müll.,
Kettering, Northamptonshire, collected by Mr. C. E. Wright,
Showing the arrangement of the tentacles and labial lobes, the genital furrow, the foot margin, the right and left lobes of the mantle separated by the partially expanded respiratory orifice, and the approximate position of the termination of the alimentary canal.

Helix aspersa has a well developed, distinct and bluntly rounded head placed at the anterior end of a narrow, oblong body, and covered with rounded and separate tubercles which show no trace of the symmetrical surface canals or facial grooves ; there are four elongate, retractile, divergent and finely granulated tentacles, the upper or posterior pair bearing the eyes at their summits, and being about four times the length of the lower or anterior pair. In other groups there may, however, be two tentacles only, bearing the eyes either at the apex or at the base according to the genus. The elongate body is covered externally by numerous tubercles or rugosities forming about sixteen more or less obliquely disposed longitudinal rows at each side of the noticeably paler and more elongate row of mid-dorsal tubercles which separate the two dorsal grooves or furrows : the ill-defined lateral or genital groove extends on the

right side from the genital orifice to the neighbourhood of the respiratory opening, the corresponding groove at the left side occupying a similar position—these are erroneously termed the Facial Grooves by Pilsbry. The colouring of the body is usually blackish grey on the upper anterior surface, but becomes whitish with ill-defined tubercles as the mantle is approached; there is also a paler area below the lateral groove, and the spreading sides of the foot or pleuropodia assume a yellowish aspect from the abundance of minute lime cells covering the tips of the tubercles in that region.

The ventral part of the body is formed by the foot or locomotor plane, a large and muscular expansion of an elongate shape, but rounded in front and terminating behind in a bluntly pointed tail; its upper surface is somewhat spread out or flattened at the sides and defined by a rather irregular longitudinal groove, which is connected with the grooves or furrows separating and forming the rugosities of the body and from which about twenty-five chief furrows descend more or less perpendicularly to the sole at somewhat irregular intervals, the interspaces being filled by flattish and irregularly shaped tubercles.

The mantle or pallium fits in a cap-like form upon the spirally coiled and protuberant visceral sac, on the back of the animal; it is of a dark translucent grey colour, besprinkled with yellowish specks, probably lime cells, and is formed by a thin and transparent fold of the integument, which becomes thicker and more exclusively glandular at the free margin or collar, which contains the principal shell-secreting cells and exhibits a colouring corresponding somewhat to the markings of the shell; it is fused to the neck of the animal and encloses anteriorly a spacious respiratory cavity, the roof of which is covered with an intricate plexus of blood vessels containing the blood undergoing oxygenation on its way to the auricle; a contractile aperture for respiratory purposes, subjacent to a distinct yellowish patch formed by thickly clustered lime cells, is situate on the right side of the body and contains posteriorly within its margins the outlets of the alimentary and renal organs, and also divides the mantle into a left or anterior lobe and a right or posterior one. The

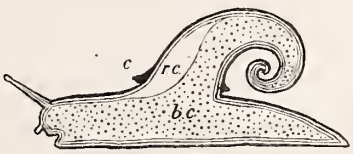


FIG. 305.—Schematic section of *Helix*, showing position of respiratory cavity, etc. *b.c.* body or visceral cavity; *c.* collar of mantle; *r.c.* respiratory cavity (after Binney).

hinder pallial margin develops the columellar lobule, a special process which forms the reflection covering the umbilicus of the shell.

The Visceral or body region is developed dorsally to the foot and abruptly protruded from its upper surface as a spirally twisted and tapering sac, enclosed by the mantle and covered by a shell of similar shape : it contains the bulk of the viscera of the animal and the reproductive glands : the length or number of whorls of the sac in the different species, corresponding to the obesity or slenderness of the visceral mass.

Internally, although the primitively symmetrical organization has been more or less destroyed by the twisting or torsion the body has undergone, yet the organs may still be grouped under the six heads proposed for the classification of the organs in mollusca generally, viz. : The Nervous, the Alimentary, the Vascular, the Glandular, the Muscular, and the Reproductive systems. The

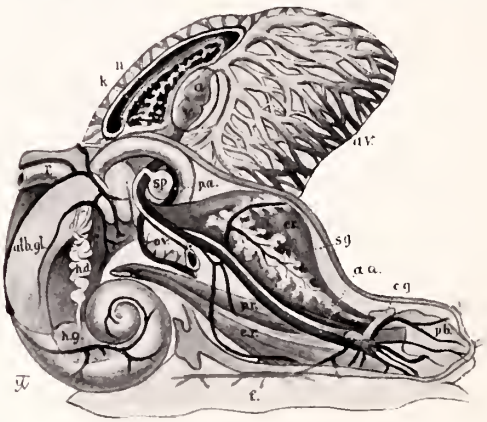


Fig. 306.—*Helix aspersa* dissected from right side with body wall and a portion of the genitalia removed to show the relative positions of some of the chief organs of the body. The kidney, the ureter, and the pulmonary chamber opened and turned back (after Howes).

a. auricle and *v.* ventricle of the heart ; *a.a.* anterior aorta ; *alb. gl.* albumen gland ; *a.v.* afferent pulmonary veins ; *c.g.* cerebral ganglia ; *cr.* crop ; *c.r.* columellar retractor ; *f.* foot ; *h.d.* hermaphrodite duct ; *h.g.* hermaphrodite gland ; *k.* kidney ; *ov.* ovispermatoduct ; *p.a.* posterior aorta ; *p.b.* pharyngeal or buccal bulb ; *p.r.* pharyngeal retractor ; *r.* rectum ; *s.g.* salivary glands ; *sp.* spermatheca ; *u.* ureter.

general and relative arrangement of the chief organs in our type does not materially differ from that of our other monœcious monotremate gastropods. The respiratory organs are anteriorly placed, with the external orifice at the right side of the body, the heart, within its pericardial chamber, being always in close connection with them and normally situate towards the left side, the renal organ being in close

proximity and actual connection with the pericardium by the ciliated reno-pericardial funnel. The alimentary canal, with its enlarged food receptacles, is convoluted chiefly amongst the lobes of the voluminous liver, which occupies most of the upper whorls of the shell, and in

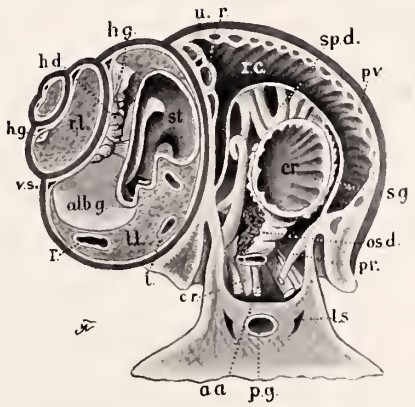


FIG. 307. — Slightly oblique transverse section in front of the columella of *Helix aspersa*, to how the arrangement of the internal organs × 2 (after Howes).

a.a. anterior aorta; *alb.g.* albumen gland; *cr.* crop; *c.r.* columellar retractor; *h.d.* hermaphrodite duct; *h.g.* hermaphrodite gland; *i.* intestine; *l.l.* anterior lobe of liver; *l.s.* lateral pedal blood sinus: *os.d.* ovispermatoduct; *p.g.* pedal gland; *p.r.* penis retractor; *p.v.* pulmonary vessels; *r.* rectum; *r.c.* respiratory cavity; *r.l.* posterior lobe of liver; *s.g.* salivary glands; *sp.d.* spermatheca duct; *st.* stomach; *u.* ureter; *v.s.* visceral blood sinus.

which are also imbedded the gonads or germinal glands; the other or accessory organs of the reproductive system are usually of a very noticeable size and have the external aperture for their functional exercise at the right side of the neck.

The NERVOUS system of *Helix aspersa* is of a highly specialized character, consisting of several more or less distinctly paired supra- and sub-œsophageal ganglionic masses, which are concentrated around the anterior end of the œsophagus and more or less completely fused together to form the nerve collar, the component ganglia of which are better studied in immature animals, as in adults they become more welded together and less clearly distinguishable. The supra-œsophageal mass is formed solely by the cerebral ganglia and the sub-œsophageal by the buccal, the pedal, and the aggregated visceral ganglia; from these conjoined centres, which are all enclosed or buried amidst a layer or sheath of connective tissue, nerves are distributed to all parts of the body.

The supra-œsophageal or cerebral ganglia, the chief seat of the sensory functions, are dorsally placed, a broad transverse commissural

band connecting its component parts above the œsophagus anteriorly. They give nerves to the head and the neighbouring organs, large nerves arising from their periphery which proceed to the ommatophores and the lips, the lower tentacles being innervated chiefly by a branch from the labial nerve; the reproductive organs are also innervated by a nerve emanating from the right side. From them also originate the three pairs of connectives which are the bonds of connection between the various groups of ganglia and form the three more or less closely approximate nerve collars surrounding the œsophagus, the most anterior being formed by the union of the cerebral and buccal ganglia, the posterior one by the cerebral and the aggregated visceral ganglia, and the pedal and cerebral centres uniting to form the central collar. The œsophagus, salivary ducts, and pharyngeal retractors pass between the cerebral and the visceral ganglia and the anterior aorta between the visceral and the pedal centres. The pedal ganglia are formed by a pair of closely apposed medullary masses united together by a broad commissure and connected with the cerebral and aggregated visceral ganglia by two pairs of connectives. The pedal ganglia are placed beneath the œsophagus and above the foot, and constitute in part the sub-œsophageal ganglionic mass, distributing nerve fibres ventrally to the locomotor foot and pedal gland and laterally to the neighbouring body wall.

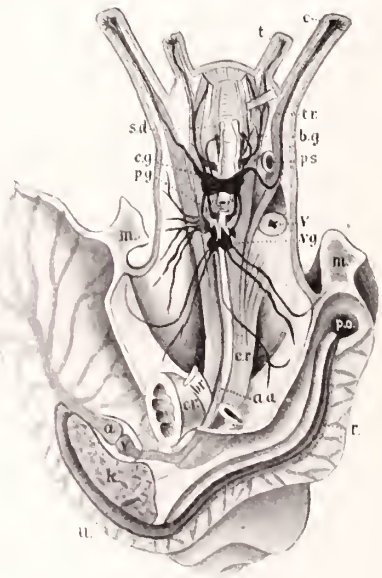


FIG. 308.—*Helix aspersa* dissected from above to show the general arrangement of the nervous system and cephalic retractors. The body has been opened to right of the renal organ, the tentacles laid open, and the crop, buccal retractor and genitalia mainly removed, but cut ends shown (after Howes).

a. auricle and *v.* ventricle of the heart; *a.a.* anterior aorta; *b.g.* buccal ganglia; *b.r.* buccal retractor; *c.g.* cerebral ganglia; *cr.* crop; *c.r.* columellar retractor; *e.* eye; *k.* kidney or nephridium; *m.* mantle; *o.* ommatophor; *p.g.* pedal ganglia; *p.o.* pulmonary orifice; *p.s.* penis sheath; *r.* rectum; *s.d.* salivary duct; *t.* anterior tentacle; *t.r.* tentacular retractors; *u.* ureter; *v.* vagina; *v.g.* visceral ganglia.

The visceral or parieto-splanchnic ganglia are formed by five more or less distinctly defined constituents, partially fused when young, but

more completely so in adults; the anterior pair, known as the pleural ganglia, are joined by connectives with the cerebral ganglia, but are in actual contact with the pedal centres and with each other; the pallial, known also as the visceral or intestinal ganglia, are placed more posteriorly and intimately fused with each other and to the more anterior pleural ganglia of their respective sides; the termination of the visceral loop is formed by an abdominal ganglion, which is closely adherent to and between the right and left pallial ganglia. This group of ganglia innervates the body wall, three sets of nerves being given off from the right and two from the left side for this purpose, which enter the tissues at the base of the visceral sac; the reproductive glands are innervated by a strong nerve from the abdominal ganglion which accompanies the posterior aorta and sends a branch to the heart; many fibres also enter and anastomose within the glandular mantle margin and innervate the mantle and its organs, and the viscera generally receive their nerve supply from this centre, which fulfils the rôle of a sympathetic system, regulating the involuntary motions of the alimentary and other organs.

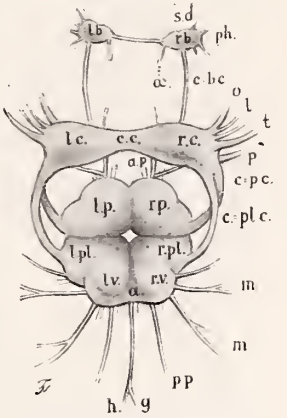


Fig. 309.—Nerve centres from a half-grown *Helix aspersa*, to illustrate the relative positions of the various ganglia and the origin and distribution of the chief nerves, highly magnified.

a. abdominal ganglion; *r.b.* and *l.b.* right and left buccal ganglia; *r.c.* and *l.c.* right and left cerebral ganglia; *r.p.* and *l.p.* right and left pedal ganglia; *r.pl.* and *l.pl.* right and left pleural ganglia; *r.v.* and *l.v.* right and left visceral or pallial ganglia; *c-b.c.* cerebro-buccal connective; *c-p.c.* cerebro-pedal connective; *c-pl.c.* cerebro-pleural connective; *c.c.* cerebral commissure; *a.p.* anterior pedal nerve; *g.* nerve to ovotestis, with *h.* branch to heart; *l.* nerves to lips; *m.* to anterior and *m'* to posterior portion of mantle; *o.* to ommatophore; *œ.* to œsophagus and stomach; *p.* to penis or male organ; *ph.* to pharynx; *p.p.* to posterior part of foot; *s.d.* to salivary ducts; *t.* to lower tentacle and lips.

The buccal or stomato-gastric ganglia are small but distinct reniform nervous masses which do not fuse together as do the various other ganglia; they are placed at the sides of the buccal cavity, near the outlets of the salivary ducts; connected by a delicate commissure passing beneath the œsophagus and joined by pigmented connectives to the under surface of the cerebral ganglia, they give off nerves to the mouth, the œsophagus and stomach.

The buccal mass has play backwards and forwards through the cerebro-visceral nerve-ring, involving the buccal ganglia in its movements, so that they may be in front or behind the cerebral ganglia, according to the state of retraction or protrusion of the buccal bulb.

The general sensibility has its seat in the whole external integument, over which fine setiform neuro-epithelial cells are profusely distributed, whose irritability renders the surface excessively sensitive to tactile impressions and probably also to other influences; its special developments are however more particularly localized in the anterior region of the body and on its exsertile appendages.

The Olfactory sense is perhaps the most important faculty possessed by the mollusca and is functionally operative and efficient at comparatively great distances; it is exercised by the olfactory organs or rhinophores, situate at the distal extremity of the dorsal or posterior tentacles, and innervated from the cerebral ganglia, the nerve from which expands on its course within each tentacle to form a large olfactory ganglion from which arise the numerous nerve ramifications terminating in the layer of epithelial olfactive cellules congregated together on the somewhat more elevated epithelium spread over the apical surface of the dorsal tentacles. It is probable, however, that the lower or anterior tentacles, which are well and similarly innervated, aid in the exercise of the olfactory sense in addition to their tactile function.

Fig. 310. — Rhinophore of *Helix pomatia*, highly magnified (after Flemming).

e. eye; *g.c.* ganglion cells; *g.s.* ganglionic layer; *ol.ep.* olfactory epithelial cellules; *ol.g.* olfactory ganglion; *op.n.* optic nerve; *pg.c.* pigment cells; *r.* eye retractor; *t.r.* tentacular retractor.

The Eyes are two in number and obliquely placed at the tips of the dorsal tentacles, hence called ommatophores or eye-bearers; they are constituted by a retina which arises from an invagination of the tegumentary epithelium and which contains sensorial and pigmented rods, arranged perpendicularly to the optic axis of the eye; the oval crystalline lens is a cuticular formation derived from the retinal epithelium and does not entirely fill the optic cavity, but is enclosed by a less dense cuticular substance, termed the vitreous body or humour. The optic nerve springs from the cerebral ganglion and reaches the optic bulb in the rear, forming an enlarge-

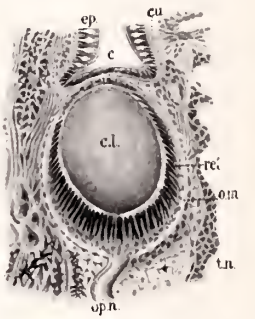


Fig. 311. — Eye of *Helix pomatia*, highly magnified (after Simroth).

c. inner cornea; *cu.* cutis; *c.l.* crystalline lens; *ep.* epithelium, becoming thin and transparent and forming the outer cornea; *o.m.* outer membrane or sclera; *op.n.* optic nerve; *ret.* retina; *t.n.* tentacular nerve.

ment or ganglion before piercing the enclosing outer coat or sclera and spreading out beneath the retina, not penetrating through and overlaying the retinal rods, as in the vertebrates and in the pallial eyes of the opisthobranchs.

The AUDITORY or Equilibrating organs, known as the otocysts, consist of a pair of convex and prominent vesicles, with a thin, colourless and transparent investment, lined internally with sensorial and ciliated epithelium, and containing, suspended in the fluid contents, numerous calcareous concretions or otoconia of variable sizes, of which 120 have been counted in the upper layers, within a single capsule, though many were overlaid and concealed and therefore uncounted. The otoconia are oval and transparent, with elongate nuclei, and vary in number according to age, being proportionately fewer in immature animals; they are always in a state of incessant oscillation, owing to the activity of the ciliated investment of the interior of the sac, although they remain persistently aggregated towards its centre, leaving a distinct space between the mass of otoconia and the walls of the capsule. The otocysts are placed upon the under-side of the pedal ganglia, at or near the posterior outer corners, though receiving their innervation from the cerebral centre, the auditory nerve running from the cerebral ganglia between the cerebro-pedal and cerebro-visceral connectives to the otocyst of their respective sides. The otocysts, in addition to the auditory function they are assumed to possess, are probably important aids in determining the orientation of the body during locomotion.

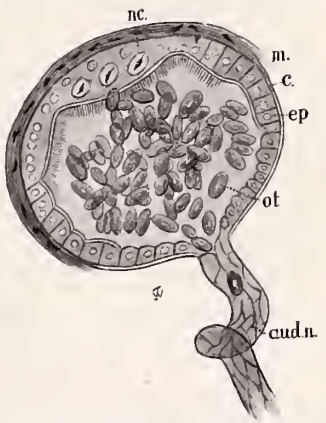


FIG. 312.—Otocyst of *Helix pomatia*, slightly compressed, showing the internal ciliated tract, etc., highly magnified (after Leydig).

aud. n. auditory nerve; *c.* cuticle; *ep.* epithelial layer; *m.* muscular layer; *nc.* epithelial cells with large fusiform nuclei; *ot.* otoconia.

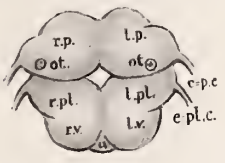


FIG. 313.—Underside of sub-œsophageal ganglia of *Helix aspersa*, showing otocysts *in situ*, highly magnified.

a. abdominal ganglion: *c-p.c.* cerebro-pedal connective; *c-pl.c.* cerebro-pleural connective; *ot.* otocysts; *r.p.* and *l.p.* right and left pedal ganglia; *r.pl.* and *l.pl.* right and left pleural ganglia; *r.v.* and *l.v.* right and left visceral ganglia.

The sense of TASTE is considered by Simroth to be diffused over the surface of the body, but to be specially localized in the terrestrial

pulmonates in the anterior part of the buccal cavity, though the oral lobes at the sides and above the mouth, which are furnished with ganglia and innervated from the anterior tentacular nerve, have also been assumed to be gustatory in function.

The ALIMENTARY system in *Helix aspersa* is formed by a muscular buccal cavity or pharynx, opening externally by a mouth or oral aperture, bounded by soft fleshy circular lips, and provided with a hard, dark brown, chitinous upper jaw, strongly convex anteriorly and broadly crescentic in shape, with attenuate and rounded ends, and a variable number of prominent vertical ribs or folds strongly denticulating both upper and lower margins, and also showing perceptible longitudinal striation or lines of increase. There is also a peculiar and somewhat prehensile apparatus of an oblong shape, termed the odontophore or radula, which is attached like a tongue to the floor of the mouth, but supported and elevated in the centre by the gristly odontophoral cartilage, and armed with innumerable and characteristically formed recurved denticles arranged in regularly curved transverse and straight longitudinal rows or series, the specimen figured having a transverse formula of 43–1–43 at its widest part.

FIG. 314. — Mandible or Jaw of an *Helix aspersa* × 8, from Christchurch, Hants.

The central tooth is always symmetrically formed with elongate basal attachment; the free upper margin is broadly reflected with a stout median cutting point or mesocone and a small lateral ectocone

FIG. 315.—Half a transverse row of the lingual teeth of an adult *Helix aspersa*, collected by Dr. Scharff near Dublin, showing the modifications in form from the symmetrical centre tooth to the quadricuspate marginals, from a highly magnified photograph by Mr. T. W. Thornton.

Showing the symmetrical median or central tooth, *c.*; the first laterals to right and left of the median tooth; the 20th and 23rd transverse rows illustrating the transition teeth; and the 31st, 36th, 41st, and 43rd teeth of the marginal series.

at each side. The laterals are decidedly asymmetrical, the inner angle of basal attachment and the inner cutting point or endocone gradually becoming deficient, but the outer cutting point or ectocone is gradually more largely developed, and eventually, as the marginals

are approached, becomes very symmetrically bifid; the mesocone also gradually becomes bifid, so that the denticles near the margins present four strongly developed sub-equal denticulations, with a narrow basal attachment; additional transverse rows are being constantly added within the radular sac at the posterior end, to compensate for the wearing away or loss of the functional portion anteriorly. The movements of this important organ are controlled by numerous extrinsic and intrinsic muscles.

The buccal cavity opens dorsally by a thin-walled œsophagus into a large, fusiform and distensible crop, usually conspicuous by the yellow colour of its contents and situate partly within the ultimate whorl of the shell; like the œsophagus and other parts of the alimentary canal,

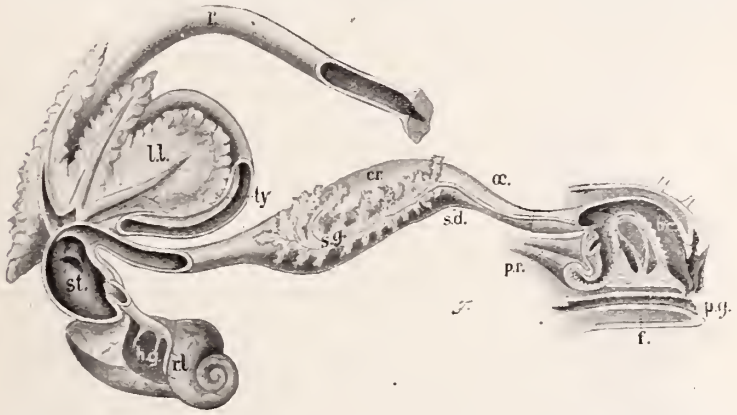


FIG. 316.—Alimentary canal of *Helix aspersa*, with appended glands, dissected out and seen from right side. The generative, circulatory, excretory, and nervous systems removed and the buccal cavity, stomach, bile ducts, intestinal canal, and pedal gland opened up (after Howes).

b.c. buccal cavity, showing radula, radular sac and jaw; *cr.* crop; *f.* foot; *h.g.* hermaphrodite gland or ovotestis; *l.l.* anterior lobe of liver; *œ.* œsophagus; *p.g.* pedal gland; *p.r.* pharyngeal or buccal retractor; *r.* rectum; *r.l.* posterior lobe of liver; *s.d.* salivary duct; *s.g.* salivary glands; *st.* stomach; *ty.* typhlosole.

its lining membrane is thrown into a series of longitudinal folds visible externally as longitudinal striation. Adherent to its sides, by fibres of connective tissue, are a pair of whitish lobulated organs, the Salivary Glands, which discharge their secretion, a soluble ferment which converts starch into sugar, into each side of the buccal cavity by means of two long and slender ducts. Beyond the crop the canal again becomes narrow, but at the loop-like extremity of the first tract quickly expands to form the simple sacculated stomach, which is slightly constricted by a longitudinal fold, and its mucous membrane also thrown into many longitudinal folds or ridges; the œsophagus enters posteriorly near the external surface and between the right and

left lobes of the liver. The pyloric orifice lies beneath and to the right of the cardiac opening, the ducts of the liver or digestive gland entering at different points.

The liver or digestive gland is the active organ of digestion and is a very large unequally bilobed gland of a reddish-brown colour, composing a large part of the visceral hump and formed by a dense aggregation of blind, branched tubules, lined by glandular epithelia. The large anterior lobe is situate immediately behind the mantle cavity and partially sub-divided into three subsidiary lobes whose ducts unite before entering the stomach a little above the pylorus. The small posterior lobe occupies the summit of the spire, opening by a large duct near the top of the stomach almost opposite to the entrance of the combined duct from the anterior lobe.

The organ is of very complicated function and structure (see p. 140, f. 298), being formed of calcareous, ferment, and hepatic or liver cells, with a quantity of fat globules interspersed; the secretions of the ferment cells are a powerful aid to the assimilation of the ingested food, as they are not only capable of digesting proteids but also assist the salivary glands in the conversion of starch to sugar. The calcareous glands contain colourless granules of carbonate or phosphate of lime, which are assumed to be eventually utilized in the formation of the shell or its epiphragm; the hepatic cells contain globules of a spherical form, which excrete small vesicles with yellowish contents.

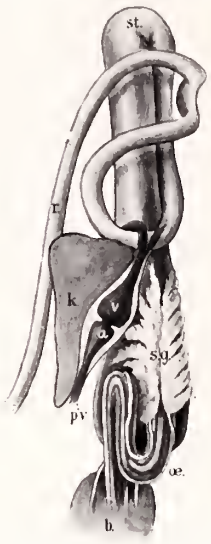


Fig. 317.—Plan of the intestinal convolutions in *Helix aspersa*, also showing how they are held in position anteriorly by the anterior aorta, and illustrating the relations of the heart and nephridium.

a. auricle of the heart; *b.* buccal bulb; *k.* kidney or nephridium; *p.v.* pulmonary vein; *r.* rectum; *s.g.* salivary glands and ducts overlying crop; *st.* stomach; *v.* ventricle from which arises the aorta.

After leaving the stomach, the intestinal canal keeps to the left side of the body, and follows an S-shaped course, imbedded within the tissues of the liver, first in an upward and forward direction, the second flexure being held in position anteriorly by the cephalic or anterior branch of the aorta; the third flexure gradually approaches the right side of the body and occupies a more dorsal position, skirting in its course the posterior margin of

the renal organ ; the final tract or rectum runs along the right margin of the pulmonary cavity, beneath the ureter, and terminates at the anus upon the posterior side of the respiratory orifice.

The Circulatory or Vascular system has for its centre and motor the heart, which in *Helix aspersa* is, as in the Gastropoda generally, divided into two chambers of approximately equal size, the auricle and the ventricle ; the auricle has delicate walls and receives the aërated blood by the pulmonary vein from the respiratory plexus and passes it forward to the pyriform muscular ventricle, regurgitation being prevented by a valvular arrangement at the junction of the vessels. The heart is confined within a thin-walled oval cavity or pericardium, placed on the left posterior side of the roof of the mantle chamber and in close and actual connection with the renal organ by the reno-pericardial funnel. The heart being exclusively occupied in propelling the blood through the system, is termed a systemic heart. The ventricle transmits the oxygenated blood received from the auricle by a single trunk or aorta, which bifurcates on entering the body cavity, dividing into an anterior and a posterior trunk ; the anterior runs parallel with the sacculated oviduct and along the right side of the crop, passing beneath the intestinal tract and the spermatheca to the right side of the body, giving branches to the salivary glands and the anterior part of the foot ; it then passes through the nerve collar between the pedal and aggregated visceral ganglia and is distributed to the buccal mass and neighbouring parts.

Fig. 318. — Heart of *Helix aspersa*, showing the connection of auricle and ventricle and indication of walls of pericardium (highly magnified).
a. auricle ; *v*. ventricle.

The posterior aorta is at first associated with the intestinal tract and mainly supplies the alimentary system and its dependent organs, running quite to the summit of the spire, contributing the blood supply to both lobes of the liver, the gonads, etc., on its course.

These distinctly defined arterial vessels break up into more minute vessels or empty themselves by funnel-shaped openings into irregular blood spaces or lacunæ amongst the connective tissue, which has hence been termed lacunar tissue (see figs. 291 and 296). These smaller blood spaces eventually unite with the large visceral sinus, which runs from the top of the spire within the thickened upper edge of the spirally-coiled visceral sac, or with one of the two large lateral sinuses

situate at the sides of the pedal gland within the foot. The lateral pedal sinuses are only indirectly, but the visceral sinus is directly continuous with the great circular pulmonary sinus, which surrounds the base of the pulmonary chamber, and adjoins the rectum, from which it receives many small veins.

From the circular pulmonary sinus the blood is distributed upon the sides and roof of the respiratory cavity, which is formed by a thin fold of the mantle and bears within or on its surface, especially anteriorly and along the right side, a very rich plexus of thin-walled blood vessels, within which the blood becomes oxygenated by exposure to the air within the respiratory chamber.

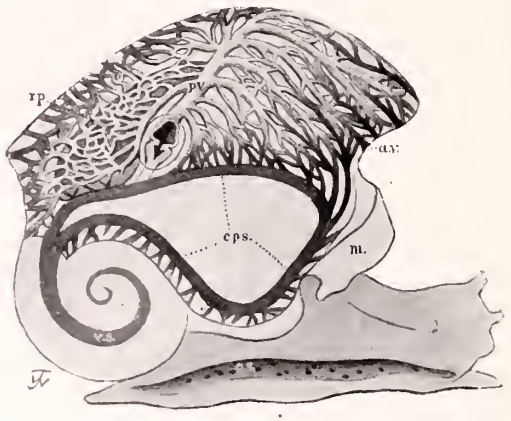


FIG. 319.—*Helix aspersa* from a dissection, after injection, to show the chief venous sinuses and the respiratory and renal capillary systems. The pulmonary sac is cut close along the rectum and turned back to show the whole pulmonary plexus at one view and the heart opened to show the interior of the auricle and ventricle. The venous vessels are all darkly shaded (after Howes).

a.v. afferent pulmonary veins carrying the blood for oxygenation to the pulmonary plexus from the circular pallial sinus, *c.p.s.*, which receives its supply chiefly from the visceral sinus, *v.s.*, and from the paired pedal sinuses, of which one is shown, *p.s.*; *m.* mantle margin; *p.v.* pulmonary vein, which receives the arterialized blood from the respiratory plexus; *r.p.* renal capillary plexus.

The afferent or incoming and the efferent or departing veins alternate with great regularity and are in intimate connection by means of a very complex and intricate series of delicate vessels, the efferent pulmonary vessels gradually uniting to form the great pulmonary vein, a large venous trunk on the roof of the respiratory cavity, conveying the arterialized blood direct to the auricle. A considerable volume of the blood, however, has a portal circulation within the tissues of the renal organ, during which the uric acid and other waste substances are eliminated from it, the blood thus purified entering the pulmonary vein by means of a large and some small veins, without fully circulating within the pulmonary plexus.

Helix aspersa, like other mollusca, has little proper heat, and is practically Poikilothermic or approximately of the same temperature as the surrounding atmosphere, becoming colder or warmer internally in accordance with, and in response to the variations of temperature to which it is exposed. The contractions of the heart are more numerous in the young than in the adult mollusk under similar conditions, but the number of pulsations has a wide diurnal range and in our ordinary summer temperatures probably varies between twenty-five and sixty-five per minute, even in the same animal, as the action is intimately related to the external temperature, being accelerated by increased warmth or active movement and diminished by cold, under which latter circumstances the contractions become more feeble, with however an occasional beat of full amplitude.

The Glandular or Secretory system, with which are included the excretory organs, are constituted of those organs or glands by which substances differing in composition from the blood and necessary for the proper exercise of the functions of the body are elaborated therefrom and utilized, or if hurtful expelled from the system. It is composed not only of the salivary and digestive glands, which assist in the processes of digestion, and the digitate, albumen, prostatic and other glands, which are adjuncts to the reproductive organs and are alluded to under the systems with which they are functionally connected, but the whole surface of the body, foot and mantle is more or less glandular and furnished with unicellular glands, of which those containing pigment give the surface of the body or its various organs their characteristic colour. There are also numerous mucus cells scattered over the whole surface, which maintain the exterior in a moist and pliant condition. A very dense aggregation of such cells exists within the Pedal gland, a medial supra-pedal invagination, which extends backward within the foot and opens anteriorly by a cleft between the mouth and foot; the contained glands secrete mucus abundantly, which is expelled by the aperture in advance of the foot and serves to lubricate the path to be taken by the mollusk.

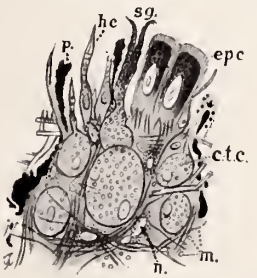


Fig. 320.—Portion of Corium and Cuticle of back of *Helix pomatia*, highly magnified (after Flemming), to show its structure and glandular nature.

c-t.c. connective tissue cells, with interspersed nuclei, *n.*; *ep.c.* cylindrical epithelial cells; *h.c.* hair cells; *m.* longitudinal and cross cut muscle fibres; *p.* pigment; *s.g.* slime or mucous glands.

The Lymphatic glands are not strictly localized in our type ; the phagocytic or lymph cells being diffused amongst the connective tissue in various parts of the body, although the function is most actively carried on within the respiratory plexus in which the lymphatic cells thickly surround the larger pulmonary vessels.

The Nephridium (νεφρός, kidney) or renal organ (see p. 146, f. 306), an important secretory and the chief excretory organ, is of an ochreous-yellow colour, and placed in the rear of the pallial cavity, between the rectum and the pericardium. It communicates with the latter by a ciliated canal, the reno-pericardial funnel, and with the exterior by a thin-walled duct or ureter, which arises at the proximal end of the kidney and runs along its right side to the distal end, returning along the right side of the mantle cavity above the rectum to the pulmonary orifice, the last tract forming the so-called secondary ureter.

The organ is of a parenchymatous and vascular character, with its internal walls thrown into a number of lamellar folds, projecting within the lumen or cavity, and is permeated by an intricate plexus of vessels through which venous blood, somewhat intermingled with arterial, circulates before reaching the auricle : its glandular secretory epithelium, which contains rounded granules or concretions, eliminates from the blood the uric acid and other substances, which are expelled from the system by the ureter.

The Muscular system is very complicated, and its constituent parts too numerous to be individually particularized. The principal, how-

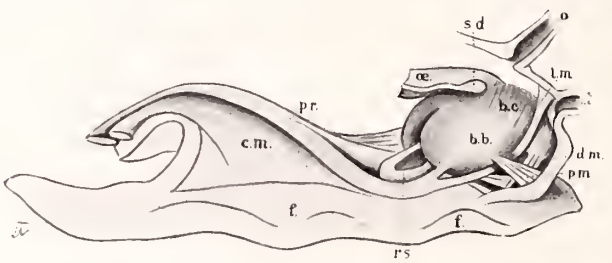


Fig. 321.—Dissection showing the general muscular system of *Helix aspersa* and the arrangement of the extrinsic muscles of the buccal bulb (after Howes).

b.b. buccal bulb ; *b.c.* constrictor muscles of buccal bulb ; *c.m.* columellar muscle ; *d.m.* depressor muscles of buccal bulb ; *f.* foot ; *l.m.* levator muscles of buccal bulb ; *o.* ommatophore ; *œ.* œsophagus ; *p.m.* buccal protractor muscles ; *p.r.* pharyngeal or buccal retractor ; *r.s.* radular sac ; *s.d.* salivary ducts ; *t.* anterior tentacle.

ever, are the retractors of the foot, those of the buccal mass and neighbouring organs, the penial retractor, the constrictor muscles of the mantle margin and of the pulmonary aperture. Of a subsidiary

but interesting character, may be mentioned the extrinsic and intrinsic muscles of the buccal bulb.

The muscles or cartilages here especially alluded to, are of a pearly glistening white and very strong and ribbon-like in character.

The columellar muscle, by which the animal is organically attached to the shell, is the largest and most important muscle of the body, and is affixed at its distal end to the columella near the commencement of the penultimate whorl (see p. 54, f. 130) and passes beneath the lung chamber, along the inner or right side of the spiral, dividing to the right and left into numerous fibres which interlace with the tissues of the foot.

Near its origin the columellar muscle gives rise to the paired tentacular retractors, each of which, prior to entering the tentacles and before re-bifurcation, gives off a broad tripartite muscle to the anterior part of the foot; the retractor of the dorsal tentacle expands noticeably before reaching the apex, while that to the lower tentacle again divides, sending a strong branch to the lip.

The pharyngeal or buccal retractor originates adjoining to and immediately in advance of the paired tentacular muscles and is formed by a powerful ribbon-like muscle, which divides before reaching the buccal bulb, to which it is attached ventrally and laterally by the expanded ends.

The Penial retractor is a powerful unpaired muscle attached to the distal end of the penis sheath and to the floor of the pulmonary chamber.

The extrinsic muscles of the buccal bulb are formed by the pharyngeal retractor and by a number of slender muscular bands, which pass from its exterior to the walls of the anterior region of the body, and in accordance with their function are distinguished as depressor, levator or protractor muscles.

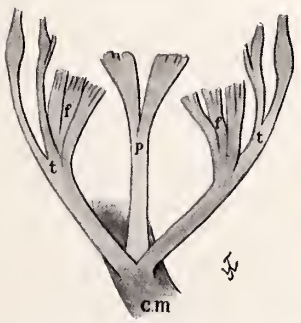


FIG. 322.—Cephalic retractors of *Helix aspersa* × 4.

c.m. columellar muscle; *f.* anterior foot retractors; *p.* pharyngeal or buccal retractor; *t.* tentacular retractors.

The intrinsic muscles are formed chiefly by the protractor and retractor fibres, attached to the radular cartilage anteriorly and posteriorly respectively, and communicating the motion to the radular membrane.

The Reproductive organs of *Helix aspersa*, like those of the Pulmonata generally, are of a hermaphrodite or monœcious character, but this hermaphroditism does not normally affect the necessity for reciprocal union to ensure the fertilization of the ova.

The Ovotestis or Hermaphrodite Gland, the essential constituent of the system, is lodged in the posterior lobe of the liver near the

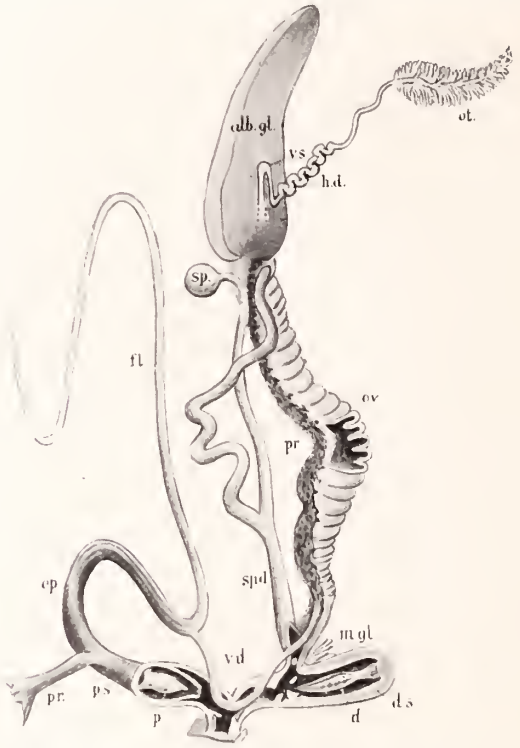


Fig. 323.—Reproductive organs of *Helix aspersa* dissected out and isolated. The penis sheath, stylophore, uterus, atrium and vagina opened up—the penis sheath to show the intromittent organ; the stylophore, the contained dart; and the uterus, its sacculate structure.

alb. gl. albumen gland; *d.* dart *in situ*; *d.s.* dart sac or stylophore; *ep.* epiphallus; *fl.* flagellum; *h.d.* hermaphrodite duct; *m.gl.* mucus glands; *ot.* ovotestis or hermaphrodite gland; *p.* penis; *p.s.* penis sheath; *pr.* prostate or sperm duct; *p.r.* retractor muscle of penis sheath; *sp.* spermatheca; *sp.d.* spermatheca duct with thick cæcal diverticulum; *ov.* uterine portion of oviduct; *v.d.* vas deferens; *v.s.* seminal vesicle or claw.

apex of the shell, and is constituted by an aggregation of converging digitate whitish lobules, on whose internal walls the female and male elements, distinguished as the Ova and the Spermatozoa originate, the former as rounded and separate cells, which continue their development, adherent to the follicular walls; while the spermatozoa are filiform bodies with enlarged heads, usually aggregated in clusters,

which are dehisced at an earlier stage from the sides of the follicle, their development proceeding within the follicular lumen. The Hermaphrodite Duct, a sinuously convoluted tube, leads from the ovotestis and conveys the ova and spermatozoa forward, but before reaching the large, linguiform and yellowish Albumen Gland it bends abruptly upon itself and forms a peculiar bent subclavate sac, known as the Seminal Vesicle or claw. The duct then enters and traverses the albumen gland, receiving therein its viscid secretion, by which the ova become enveloped; on the emergence of the duct therefrom, the ova and spermatozoa are separated and flow within special channels, the Sperm Duct and the Uterus, which, though united exteriorly, are separated internally by two closely superposed longitudinal septa. The uterus is of a clear bluish-white colour, with strongly sacculate and voluminous glandular folds, but the walls of the sperm duct are formed by an aggregation of ochreous-white prostatic follicles. As the conjoined ducts approach the anterior end of the body, the two channels separate or become diaulic, the sacculated uterus becoming straight and thick-walled and distinguished as the Oviduct; while the sperm duct becomes a slender tube, termed the Vas Deferens, and conveys the seminal fluid to the male organ, passing beneath the right tentacular retractor and becoming buried in the tissues of the body wall for a short distance before joining with the distal epiphallial prolongation of the penis sheath, which is still further extended by a long and slender hollow filament, termed the Flagellum, within which the Spermatophore, a peculiar and characteristic filament of agglutinated spermatozoa is formed. The Penis Sheath is a bluish-white and somewhat muscular tube, opening into the common vestibule or atrium close to the external aperture, which is placed in the nuchal region, beneath the

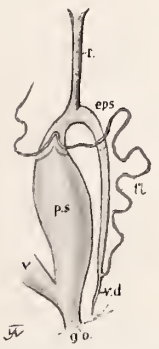


FIG. 324.—Penis sheath, epiphallus, and flagellum of *Helix aspersa* ×3, showing the mode of connection with the vas deferens.

eps. epiphallus; *fl.* flagellum; *g.o.* common genital orifice; *p.s.* penis sheath; *r.* penial retractor; *v.* vagina; *v.d.* vas deferens.

FIG. 325.—Spermatophore of *Helix aspersa*, with more highly enlarged sections, showing the structure of the anterior and posterior portions (modified after Moquin-Tandon).

right dorsal tentacle, whose retractor muscle passes between and separates the male and female organs; a powerful retractor muscle also arises from the distal end of the penis sheath and is attached medially to the floor of the lung chamber.

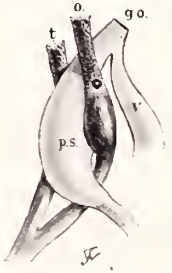


Fig. 326.—Portion of the Reproductive organs of *Helix aspersa*, showing the separation of the male and female organs by the retractor muscle of the right ocular tentacle × 3.

o. right ommatophore and its retractor; *p.s.* penis sheath; *v.* vagina; *t.* lower tentacle and retractor; *g.o.* common genital orifice.

The Spermatheca is a red-brown globular vesicle, fixed by its neck to the distal end of the ovispermatoduct and also complicated by the attachment of a muscle from the columellar retractor; it opens into the upper part of the vagina, by means of a long hollow stalk, which gives off about midway a long and thick cæcal diverticulum, about the same length as the flagellum, which is fixed terminally at the base of the albumen gland, and within which is lodged the spermatophore received during pairing from its partner in the sexual act.

The mucous glands or multifid vesicles, are paired tufts, each composed usually of about 25 tassel-like tubular glands, which open into the vagina below the spermatheca: their secretion is rich in calcic substances, which have been assumed to assist in forming the outer egg envelope.

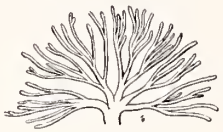


Fig. 327. Fig. 328.

Digitate Mucous Glands of *Helix aspersa* × 2.

Fig. 327.—An unusually ramose gland, bearing 46 branchlets.
Fig. 328.—A very sparsely digitate one, with 14 branchlets only.

The large, pyriform, muscular dart sac or Stylophore is situate just beneath the paired mucous glands and opens into the vagina slightly above the vestibule or atrium, and serves for the protection of the dart, which it also secretes and protrudes. It is formed chiefly of two layers; a thick, translucent, greyish-white outer coat, composed of annular and longitudinal muscle fibres, and a thinner and more vascular inner layer: the less muscular distal end bears a small subconical tubercle with some closely apposed longitudinal rods at its sides, which serves as the point of attachment for the base of the Dart or spiculum amoris, whose point is thus directed towards the aperture. This curious weapon, which is soft and flexible when removed from the sac, has a slightly curved, hollow, calcareous, and pointed stem, somewhat expanded at the base, which fits upon and is

slightly attached to the distal tubercle, and is strengthened by four projecting and slightly twisted longitudinal blades, placed at right angles to each other and slightly thickened and rounded at the outer edges, which cause the dart to revolve slightly during its protrusion. The blades gradually diminish towards the point of the dart and more abruptly basally, and are connected together at intervals by crescentic and very thin calcareous films. The dart is everted, and used by the animal as an excitant to its prospective mate, during the amorous preludes which lead up to, and precede sexual congress.

FIG. 329.—Dart of *Helix aspersa* × 4, Christchurch, Hants.

The PELECYPODA, on the other hand, differ widely from the Gastropoda, as they are exclusively aquatic animals which would appear to have adopted a more or less inactive and sedentary life, and retained more completely than the Gastropoda the original bilateral symmetry of their external and internal organs, but lost by degeneration or atrophy such organs as were especially adapted to an active locomotory existence, the probability of their former possession of such organs being corroborated by brief traces of their existence during larval life. The great development of vibratile cilia over the free surface, more especially of the largely developed and paired ctenidia or gills, render it probable that the continuous flow of food-laden currents directed towards the mouth by their action, would also tend by the easy nutrition thus secured to confirm the sedentary habits of the animal and contribute to the degeneration of the cephalic region by rendering it functionally unnecessary. The development of the ample mantle lobes and their encompassing and protecting shells becomes a necessary corollary of the adoption of inactive habits, as the degeneration of the locomotory organs would naturally prevent active escape from apprehended danger.

The Pelecypoda are broadly divided into three groups, viz.: Isomya, Heteromya, and Monomya, characterized by the relative degree of development of the adductor muscles of the shell, and which like the nerve cords in the Gastropoda equally indicate successive stages of specialization.

The Isomya are distinguished by the approximately equal size of the anterior and posterior adductors (see p. 10, f. 11); the Heteromya by the reduction in size and importance of the anterior and the increased size and importance of the posterior adductor (see p. 10, f. 12); and the Monomya, of which we have no representative in our freshwater fauna, by the anterior adductor being atrophied in the adult forms, and the posterior adductor only being developed.

The Isomyate *Anodonta cygnea* or *anatina*, which we may regard as typifying the Pelecypoda, has a more or less oval and laterally compressed form, enclosed by ample lateral mantle lobes which secrete upon their external surface a corresponding pair of shelly valves, united together dorsally by a somewhat elastic chitinous ligament, whose action tends to keep the valves apart ventrally, their closure being effected by a pair of powerful adductor muscles passing through the body and attached to the inner surface of the valves.

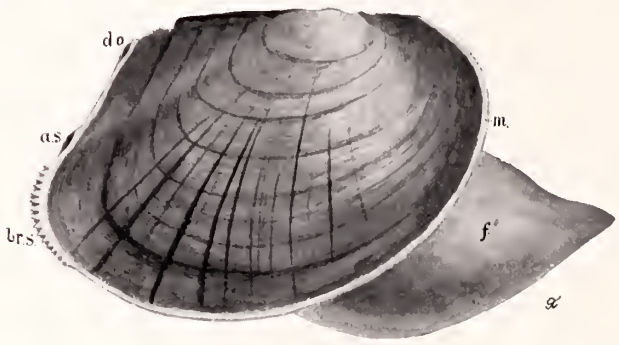


FIG. 339.—*Anodonta anatina*, showing the extended mantle lobes, the anterior position of the protrusible foot and the posterior and relative positions of the dorsal orifice, and the branchial and anal siphons, as typical of the Pelecypoda.

a.s. anal or excurrent siphon; *br.s.* branchial or incurrent siphon; *d.o.* dorsal orifice; *f.* foot; *m.* mantle margin.

The EXTERNAL FEATURES of *Anodonta* may, as in *Helix*, be examined according as they belong to the Cephalic, the Pallial, the Pedal, or the Visceral regions.

The Cephalic region is degenerate and there are no cephalic eyes. The oval mouth is without prehensile or masticatory organs, but is surrounded by large and highly vascular palps or lips, richly supplied with nerves and externally clothed by strong vibratile cilia, whose action directs the food-laden currents to the mouth.

The Pallial region, in our type, reaches a great development, being formed by two large, thin, transparent, and internally ciliated, leaf-like

folds, which completely envelop the entire body of the animal to which they are dorsally and laterally attached, but open ventrally, and enclosing between them the pallial cavity, which, by the fusion of the gill lamellæ, is divided into an upper or supra-branchial and a lower or infra-branchial chamber; in the latter are situate the foot, the gills, the palps, the oral orifice, etc., while the rectum, the renal and the genital organs open into the supra-branchial or exhalent chamber. The mantle is formed of interlaced contractile muscular fibres and connective tissue, enclosing large and important blood spaces, which seem to be in correlation with the largely developed foot.

The margins of the mantle were probably primitively entirely open, but in our type are fused together on the posterior margin, forming the branchial and the anal orifices, and hence such species are distinguished as biforate. This fusion separates the pure in-coming infra-branchial stream from the excurrent supra-branchial one laden with effete substances and excreta.

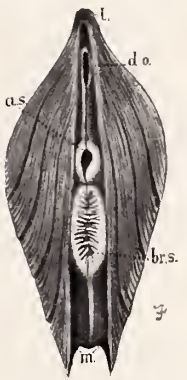


FIG. 331.—Posterior aspect of *Anodonta cygnea* to show the relative positions of the external orifices and the mode of closure of the branchial siphon by the infolding of the digitate filaments (after Howes).

a.s. anal siphon; *br.s.* branchial siphon; *d.o.* dorsal orifice; *l.* ligament of shell; *m.* mantle.

The branchial is the largest and most ventral opening and is continuous with the general mantle cleft, but may be functionally limited by the close apposition of the mantle margins.

The anal opening exhibits a subsidiary fusion by which two outwardly distinct, but internally connected apertures, are formed, the one adjoining the branchial siphon and opposite the anus is the true anal siphon; the more dorsal opening is known as the renal and also as the dorsal orifice, but the significance of its separation or the duty it performs is not as yet understood.

The local modification of the pallial margin, to form the branchial and anal siphons with definitely localized sensitive processes is in a large degree correlated with the activity of the animal, the circumscribed area they occupy showing that a part of the body is usually concealed in the mud; while the greater development of the sensitive processes around the inhalent opening enables the mollusk to detect the presence and guard against the inhalation of injurious or distasteful substances.

The Pedal or foot region is anteriorly placed upon the ventral side of the body, and is a large laterally compressed and strongly ciliated muscular appendage or protuberance, acutely angulated below and terminating in a pointed and sensitive tip, bearing on its posterior margin three minute pit-like depressions, which are the openings of mucous glands, and of the degenerate byssal gland, but have been assumed by some to be the external orifices of a water vascular system. It is capable of protrusion greatly beyond the shell by means of blood pressure, but is withdrawn by muscular contraction; and is especially adapted for forcing its way through mud and sand by alternate expansion and contraction, being noticeably stronger in those forms which habitually plough through or burrow within the mud or sand.

The Visceral sac or region is compressly oval, and quite concealed by the overlapping mantle lobes, but, as in the Gastropoda, it contains the liver, the genital glands, the convolutions of the alimentary canal, the circulatory organs, the renal organs, etc.; along each side, above the base of the foot, is a vascular longitudinal ridge, from each of which depends a pair of long reflected branchial leaflets, which originate behind the labial palps and pass backwards; and whose modifications have been ably used by Prof. Pelseneer as a basis for the classification of the Pelecypoda.

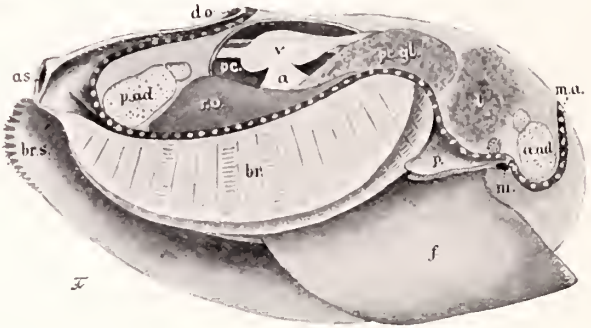


FIG. 332.—*Anodonta cygnea*, with the right mantle lobe removed and pericardium opened to show the general and relative arrangement of the organs of the body (modified after Howes).

a. auricle of the heart; *a.ad.* anterior adductor; *a.s.* anal siphon; *br.* branchiæ, with posterior suspensory ligament; *br.s.* branchial siphon; *d.o.* dorsal orifice, in connection with the anal siphon; *f.* foot, with the three pit-like depressions on the posterior margin indicated; *l.* liver or digestive gland; *m.* mouth; *m.a.* line of attachment of mantle to visceral mass; *p.* palps; *p.ad.* posterior adductor; *pc.* pericardium; *pc.gl.* pericardial gland or Keber's organ; *r.o.* renal organ or kidney; *v.* ventricle of the heart.

The INTERNAL ORGANIZATION of our type has retained the primitively paired character that distinguished its hypothetical ancestor, such organs as are not symmetrically paired being placed along the medial

line. The nervous system is also of a paired character, but with the different centres widely separated and developed correspondingly to the morphological changes in the animal. The alimentary system is convoluted more or less medially, the mouth being placed in the middle line anteriorly beneath the anterior adductor, the termination of the digestive system being at the posterior end of the body. The circulatory organs are dorsally placed, the ventricle in the median line, and enclosing the rectum, with a symmetrically placed auricle at each side, which receives the blood from the branchiæ adherent to the same side of the body. The glandular system, when localized in definite organs, is also distinctly paired, the liver being formed of two lobes and the excretory nephridial and pericardial glands have their component parts placed to the right and left of the median line. The muscular system partakes strongly of the same bilateral uniformity, the various muscles or retractors arising from one side of the body having their counterparts at the other. The reproductive organs are also paired, genital glands being present at both sides of the body, and each furnished with a duct debouching into the cavity of the inner gill of their respective sides.

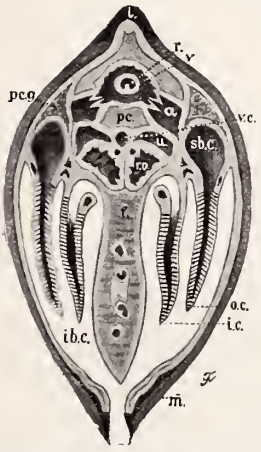


FIG. 333.—Transverse section through the middle pericardial region of *Anodonta cygnea* to show the internal structure and arrangement of the organs (after Howes).

a. auricle of the heart; *f.* foot, showing the cut sections of intestinal tract; *i.c.* inner ctenidium or gill, with supra-branchial chamber open to and continuous with infra-branchial chamber, *ib.c.*; *l.* ligament of shell; *m.* mantle lobes, lining valves and showing marginal pallial muscles; *o.c.* outer ctenidium; *pc.* pericardium; *pc.g.* pericardial gland or Keber's organ: *r.* rectum, with typhlosole; *r.o.* renal organ or organ of Bojanus, and showing the paired cerebro-pleuro-visceral commissures; *sb.c.* supra-branchial chamber; *u.* ureter; *v.* ventricle of the heart; *v.c.* vena-cava or great central blood vessel.

All the organs of the body may be advantageously studied, as in the Gastropoda, in connection with the particular system to which they have the most intimate relations.

The NERVOUS system of *Anodonta* is of the simplest type, in which well-marked ganglia exist, and is composed of three chief medullary masses or ganglia, which are placed at considerable distances from each other, but connected by long nervous cords, forming two very long nerve rings or nerve loops, which, however, evidently confer a

very efficient inter-communication between the different ganglia, as the least peripheral irritation leads to instant combined action of mantle edge, foot and shell.

The Cephalic or Cerebral ganglia, or more correctly Cerebro-pleural, as the pleural ganglia are intimately fused with the cerebral in this group, represent the supra-œsophageal ganglia of *Helix*, and are of comparatively feeble development in correlation with the atrophy of the head and the absence of the accompanying sensory organs. They are placed just beneath the skin at the sides of the oral aperture and

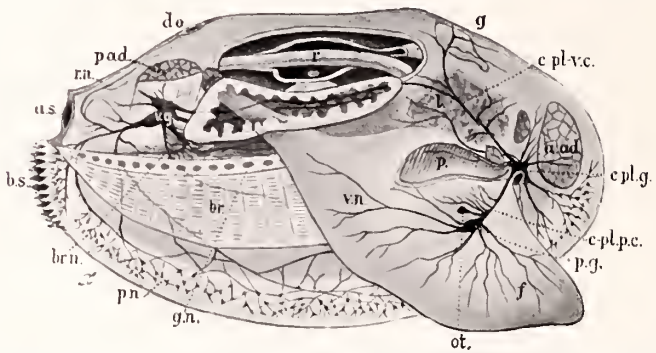


FIG. 331.—*Anodonta cygnea*, showing the disposition of the ganglia and the general arrangement and distribution of the dependent nerves, as seen from the right side after removal of the right mantle lobe, and the right ctenidia; the pericardium, the ventricle, and the right nephridium opened up (modified after Duvernoy, Howes and others).

a.ad. anterior adductor; *a.s.* anal siphon; *br.* branchia; *br.n.* branchial nerve; *b.s.* branchial siphon; *c-pl.g.* cerebro-pleural ganglia; *c-pl.p.c.* cerebro-pleuro-pedal connective; *c-pl.v.c.* cerebro-pleuro-visceral commissure; *d.o.* dorsal orifice; *f.* foot, with ramifying pedal nerves; *g.* gastric nerve; *g.n.* genital nerve; *l.* liver or digestive gland; *ot.* otocyst; *p.* palps; *p.ad* posterior adductor; *p.g.* pedal ganglia; *p.n.* pallial nervous plexus, showing numerous small ganglionic enlargements and the general anastomosis of the anterior and posterior pallial nerves; *r.* rectum; *r.n.* nerve to rectum; *v.g.* visceral or parieto-splanchnic ganglia; *v.n.* visceral nerves from pedal centre.

immediately below and in front of the pedal-protractor muscle, just above the attachment of the mantle lobes, and connected together by the cerebral commissure passing above the mouth; they innervate the palps, the anterior adductor, the region around the mouth and the anterior part of the mantle.

The Pedal ganglia are also paired, although the constituents are fused together: they are imbedded at the root of the foot, near the junction of the muscular with the visceral part, but rather distant from the cerebro-pleural centre, to which they are joined by straight connectives, which are easily dissected out. The size of these ganglia is always in direct correlation with the development and functional importance of the foot.

The Pleuro-pedal connectives, which have been hitherto considered to be a characteristic peculiar to the Gastropoda, are present in our type, but fused with the cerebro-pedal connective, forming the composite or compound nervous-cord, distinguished as the cerebro-pleuro-pedal connective.

The Visceral, Osphradial, or Parieto-splanchnic ganglia are the largest in the whole system, and are really composite ganglia formed by the fusion of several ganglionic masses, the more or less complete conjunction of the constituent ganglia being correlated with the greater or less degree of fusion which the bilateral gills have undergone; these ganglia are superficially placed, and merely covered by the tegumentary epithelium; they innervate the branchiæ, the siphons and the siphonal chamber, the posterior adductor, the posterior part of the mantle, and the heart, which is supplied by a nerve passing around the adductor. The nerve trunks from the visceral ganglia innervating the posterior portion of the mantle and those from the cerebro-pleural ganglia, which innervate the anterior part, fuse or anastomose together and form a marginal pallial nerve with an intricate plexus of ramifying nerve fibrils and small ganglionic enlargements.

FIG. 335. — Transverse section through anterior region of *Anodonta cygnea* to show the relation of the mouth and labial palps and the position and arrangement of the cerebro-pleural and pedal ganglia (after Howes).

a.ad. anterior adductor; *c.c.* cerebral commissure; *c-pl.g.* cerebro-pleural ganglia; *c-pl-p.c.* cerebro-pleuro-pedal connective; *f.* foot; *l.p.* labial palps; *m.* mouth or oral aperture; *p.g.* pedal ganglia.

The Cerebro-pleural connective is lost owing to the intimate fusion of the cerebral and pleural ganglia, and I therefore regard the long nervous cords joining the cerebro-pleural and the visceral ganglia, as commissures, and as really joining the pleural constituents of the cerebro-pleural ganglia with the visceral centre; they run close together between the anterior protractor and retractor muscles and the anterior end of the pericardium, and traverse the inner surface of the renal organs; they then diverge, passing outside the posterior retractors, and proceed to join the visceral ganglia. At the point of divarication of each commissure there is a ganglionic enlargement, which Moquin-Tandon considered to be a genital and Huxley a subsidiary visceral ganglion.

The Stomato-gastric or buccal ganglia, which are so apparent in the Gastropoda, are not differentiated in *Anodonta*, but in correlation with the atrophy of the protrusible head region have probably become degenerate and intimately fused with the neighbouring cerebro-pleural ganglia ; the visceral commissures now giving origin to some slender nervous fibrils, which reach the alimentary canal, although splanchnic nerves also arise from the chief centres.

The Sensory organs in our type are not of a highly specialized character. The general surface is, however, richly supplied with a number of epithelial sensory cells of the same character as those found in the mollusca generally, and, in addition, there are some larger cells bearing tufts of sensory hairs and known as "brush" cells, which are particularly noticeable in the Pelecypoda. The perception of tactile impressions is most keenly exercised by the papillæ or tentacular processes surrounding the branchial siphon, but the perception of touch is functionally active and efficient in other exposed parts of the body. The labial palps, although enclosed within the shell, have probably a subsidiary tactile function, guarding the oral orifice against the entrance of manifestly unlikely substances.

Fig. 336.—"Brush" Sensory Cells, highly magnified (after Sochaczewer).

The Auditory or Equilibrating organs of *Anodonta* are formed, as in *Helix*, by a pair of small closed vesicles or otocysts, which in *Anodonta* are placed near to but not in contact with the pedal ganglia, and connected by an auditory nerve to the cerebro-pleural ganglia of their respective sides. The otocysts are imbedded in connective tissue and each surrounded by an investing membrane. The walls interiorly of the cysts are formed of intermingled sensory and ciliated epithelial cells, which also secrete the limpid fluid which fills the sacs and within each of which one large calcareous concretion or otolith is suspended and kept in incessant motion by the action of the vibratile ciliated investment. The otocysts are, however, not

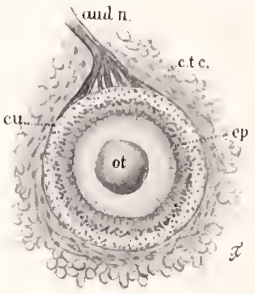


Fig. 337.—Otocyst of *Anodonta cygnea*, highly magnified (after Simroth).

aud. n. auditory nerve ; *c.t.c.* connective tissue cells ; *cu.* cuticle or enclosing membrane ; *ep.* ciliated and sensory epithelial cells, supported upon cellular tissue ; *ot.* otolith.

always symmetrically developed, but when one otocyst only exists, as occasionally happens, it is found to uniformly contain two otoliths.

The Olfactory sense is located more especially on the roof of the branchial siphon at the base of the gills near the external orifice, but is not exercised by distinctly differentiated or externally visible organs, but by elongated epithelial sensory cells overlaying a portion of the visceral ganglia, although innervated by a nerve from each of the cerebro-pleuro-visceral commissures, which are said, however, to really originate from the cerebral ganglia. The special function of this organ has been considered to be to examine the inflowing current of water which bathes the gills and brings nutriment to the mouth.

The Gustatory sense is probably not at all or very little exercised, as no discrimination appears to be made in the selection of food particles from the general substances brought by the current, except such supervision as is exercised by the labial palps.

Cephalic Visual organs are not present in the adult *Anodonta*, but traces of such eyes are probably present during the early stages of development, but these, if present, afterwards disappear, as when covered by the shell they are useless and unnecessary ; the animals are, however, acutely sensible to light and shade, the exposed surface being able to discriminate and discern the distinction and respond to it.

The Alimentary system has its anterior opening in the transversely oval mouth or oral aperture, which is placed beneath the anterior adductor muscle, and dorsally to the origin of the foot and surrounded by an anterior or dorsal and a posterior or ventral lip, which are continuous with the lining membrane of the mouth and gradually expand on each side to form the somewhat triangular palps, which are transversely ribbed on their inner faces and beset with vibratile cilia, producing a current and conveying food particles along the ciliated groove at their base, which leads towards and into the mouth, the animal being totally dependent for sustenance upon the minute organisms and food particles brought thereby. The mouth is

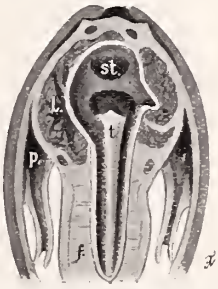


Fig. 338.—Transverse section through the anterior region of *Anodonta cygnea*, to show the relations of the stomach, the liver and its ducts and the origin of the typhlosole of the first tract of the alimentary canal (after Howes).

f. foot, with the first tract of alimentary canal ; *l.* liver, surrounding stomach and showing the bile ducts on the left side ; *p.* labial palps ; *st.* stomach, showing entrance of œsophagus, etc. ; *t.* typhlosole.

deficient of prehensile or masticatory organs and leads directly upwards by a short and distensible œsophagus to the irregularly oval stomach, which lies in front of the pericardium and with the œsophagus is imbedded within the digestive gland ; the stomach has thin walls with a caducous, cuticular lining, the *flèche tricuspide*, which overlays and protects the secretory cellules : there is also a pyloric cæcal diverticulum opening on the right side which can be closed up, and contains a gelatinous and transparent rod-like body, the Crystalline Style, a freely projecting extension or prolongation of this cuticular stomachal investment which is most distinctly developed in spring.

The Digestive tract is convoluted within the visceral sac, especially amongst the lobes of the enormous genital glands and in the tissues above the foot : it originates from the ventral wall of the stomach, passing slightly to the left side during its downward and somewhat backward course, it then curves upwards somewhat parallel to the posterior margin, and on approaching the pericardium bends abruptly

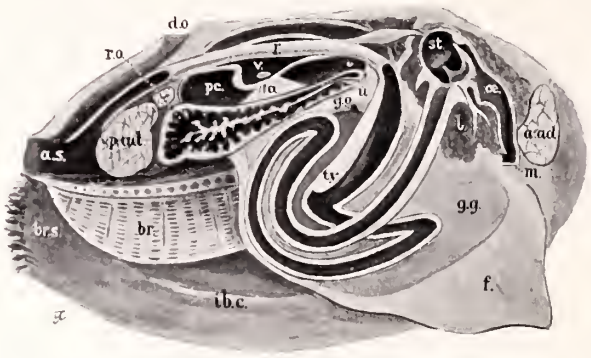


FIG. 339.—*Anodonta cygnea* dissected to show the arrangement and convolutions of the alimentary system ; the right pallial lobe, branchiæ and palps have been removed and the alimentary canal, ventricle of the heart and nephridium opened up to show their internal structure (after Howes).

a. auricle of the heart ; *a.ad.* anterior adductor ; *a.s.* anal siphon ; *br.* branchiæ ; *br.s.* branchial siphon ; *d.o.* dorsal orifice ; *f.* foot ; *g.g.* genital gland ; *g.o.* genital orifice ; *ib.c.* infra-branchial chamber ; *l.* liver or digestive gland, with bile ducts opened up ; *m.* mouth ; *œ.* œsophagus ; *p.ad.* posterior adductor ; *pc.* pericardial chamber, showing the left reno-pericardial orifice near the anterior end ; *r.* rectum ; *r.o.* renal organ or organ of Bojanus *st.* stomach ; *ty.* typhlosole of rectum ; *u.* ureter ; *v.* ventricle of heart.

backward upon itself, returning to the base of the foot on a course parallel to but outside the first upward tract, it again becomes abruptly bent upwards, traversing the body in a backward direction and on the right side of the body, gradually bending forward as the final tract or rectum towards the antero-ventral region of the pericardium, which it penetrates, passing through the ventricle and emerging from the postero-dorsal surface of the pericardium, afterwards run-

ning parallel to the postero-dorsal margin of the shell above the posterior adductor and terminating in the shallow cloacal cavity of the supra-branchial chamber.

The whole intestinal tract is lined by ciliated and glandular columnar epithelium, the absorptive surface being greatly increased, especially in the first and the terminal tracts, by the presence of the typhlosole, an internal, thick, yellow, longitudinal ridge, formed by a strong infolding of the ventral walls.

The digestive gland or liver is a somewhat symmetrical multilobed and greenish-brown organ, composed of numerous brown branched

FIG. 340.—Tubule of Liver or digestive gland of *Anodonta anatina*, highly magnified (after Vogt and Yung).

cu. cuticle; *en.* endothelium; *l.c.* lime cells, containing numerous refractive corpuscles, some enclosing pigment granules.

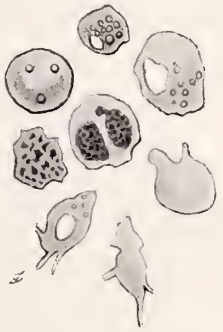


FIG. 341. — Some elements of the liver of *Anodonta anatina*, isolated and highly magnified (after Vogt and Yung).

tubules, with hepatic, ferment and lime cells, as in *Helix*, and lined with glandular cuboidal epithelial cells, with brown granular contents. It opens into the stomach by two large and several smaller ducts. As in *Helix*, the secretions probably change starch to sugar, proteids to peptones, and emulsifies the fatty foods.

The CIRCULATORY system is, as in *Helix*, composed of definite arterial and venous vessels and of an inter-communicating system of lacunar spaces. The heart, the pulsatile centre of the circulation, is a yellowish sac placed near the hinge of the shell, within the spacious and elongate pericardium, and is formed of a median ventricle and two symmetrical and laterally disposed auricles.

The auricles are paired, triangular, thin and somewhat transparent sacs, with their apices attached to the opposite sides of the ventricle, the broad basal ends receiving the blood aërated within the branchiæ and pallial lobes of their respective sides, which they transmit to the

ventricle by synchronous contractions, regurgitation being prevented by the large pocket-shaped flaps at the point of junction, distinguished as the auri-ventricular valves.

The ventricle, which receives the blood from the auricles, is a medially placed vessel, of an elongate and pyriform shape, with the thick and somewhat bilobed end directed posteriorly; it has thick, spongy and muscular walls formed of interlaced muscle fibres, and gives origin to a large arterial trunk at each end, distinguished in accordance with their respective positions as the anterior or the posterior aorta, which transmit to the body the arterial blood expelled from the ventricle by the strong and successive waves of contraction which pass rhythmically from one end of the vessel to the other.

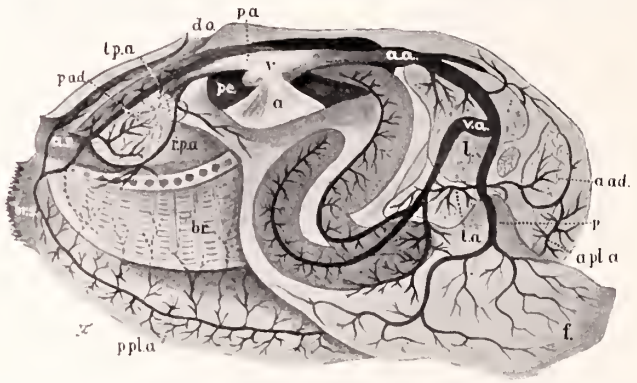


FIG. 312.—*Anodonta cygnea*, injected from the ventricle to show the arterial system. The right pallial lobe, gills and mesosoma partially removed and pericardium opened (after Howes).

a. auricle of heart; *a.a.* anterior aortic bulb; *a.s.* anal siphon; *a.ad.* anterior adductor; *a.pl.a* anterior pallial artery; *br.* branchiæ or gills; *br.s.* branchial siphon; *d.o.* dorsal orifice; *f.* foot; *l.* liver or digestive gland; *l.a.* labial artery; *l.p.a.* left posterior artery; *p.* pedal artery; *p.a.* origin of posterior aorta; *p.ad.* posterior adductor; *p.pl.a.* posterior pallial artery; *r.p.a.* right posterior artery; *v.* ventricle of heart; *v.a.* visceral artery.

The anterior aorta runs forward above the intestine, which it partially encloses, breaking up into various arteries, the two principal being the visceral artery, which supplies the intestines, the digestive and genital glands, and the pedal artery, which passes through the cerebro-pleuro-pedal nerve loop and supplies the foot, which is rendered turgid and protrusible by blood pressure, the revulsion or reflux of the contained blood towards the ventricle, which takes place upon any sudden contraction or withdrawal of the foot being arrested by a valvular arrangement in connection with the anterior aortic bulb; while the anterior pallial artery supplies the oral lobes and spreads out over the anterior part of the mantle and unites within the mantle margin with the posterior pallial arteries.

The posterior aorta is also furnished with a valvular arrangement preventing the reflux of the blood to the ventricle, and has a backward course beneath the rectum, soon dividing into two large lateral trunks, the right and left posterior pallial arteries, whose principal

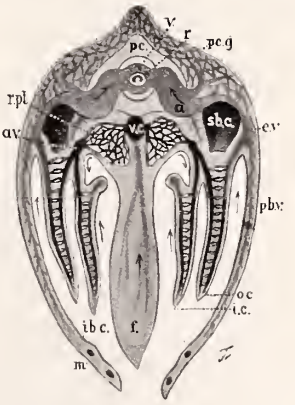


Fig. 343.—Transverse and somewhat diagrammatic section through the middle pericardial region of *Anodonta cygnea*, after injection, to illustrate the circulation within the branchiæ, renal organ, pericardial gland, and pallial lobes, and also showing the open communication between the infra-branchial chamber and the supra-branchial cavities of the inner gills (after Howes). The vessels containing venous blood are black, except the efferent pedal veins, and the arrows indicate the direction of the blood currents.

a. auricle of the heart; *a.v.* afferent branchial trunk; *e.v.* efferent branchial and pallial trunk; *f.* foot, showing the efferent pedal vein and its junction with the vena-cava; *ib.c.* lower or infra-branchial chamber; *i.c.* inner ctenidium or branchia; *m.* mantle lobes, showing pallial blood vessels, *pb.v.*; *o.c.* outer ctenidium or branchia; *pc.* pericardium; *pc.g.* pericardial gland, showing capillary plexus; *r.* rectum, showing typhlosole; *r.pl.* renal capillary plexus; *sb.c.* supra-branchial chamber; *v.* ventricle of the heart *v.c.* vena-cava, or central venous blood sinus.

branches run along the free edge of the mantle, anastomosing therein with the anterior pallial vessels, but which early give off smaller vessels, supplying the rectum, the pericardium, the posterior adductor, the siphonal retractors, and neighbouring tissues.

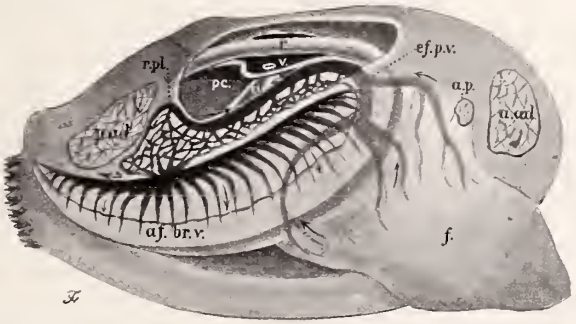


Fig. 344.—*Anodonta cygnea*, injected to show the larger vessels in connection with the venous system, especially in relation to the plexus within the renal organs. The right mantle lobe removed and the external gill lamina, pericardium and ventricle opened up (after Howes).

a. auricle of the heart; *a.ad.* anterior adductor; *a.p.* anterior protractor muscle; *af.br.v.* afferent branchial veins distributing blood within the gills; *ef.p.v.* efferent pedal veins, continuous above the nephridia with the vena-cava, the dotted line approximately indicating the position of Keber's valvule; *f.* foot; *p.ad.* posterior adductor; *pc.* pericardial chamber; *r.* rectum, passing through ventricle; *r.pl.* renal capillary plexus; *v.* ventricle of heart opened up to show the junction of the auricle and the relations of the rectum.

After permeating the body, the blood eventually reaches the venous sinuses, of which the principal are the pallial, the pedal and the great longitudinal central blood vessel or Vena-cava, which represents the circular pulmonary sinus of *Helix*, and lies between the pericardium

and the foot, and to which many other vessels converge. It is continuous with, but separable from, the pedal sinus by the powerful sphincter muscle, known as Keber's valvule, the action of which renders possible the rapid turgescence of the foot. From the vena-cava the greater part of the blood flows through and irrigates the renal organ and is then gathered up into the afferent branchial trunk at the common base of the gills and from thence distributed by smaller vessels to become arterialized by respiration within the branchial

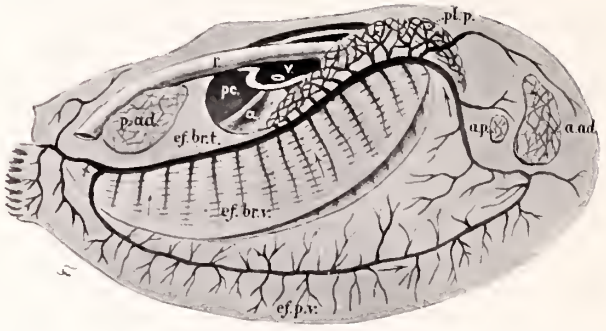


FIG. 345.—*Anodonta cygnea*, with the foot and the right mantle lobe removed, injected from auricle, to further illustrate the circulatory system, and more especially the efferent pallial, branchial and related vessels, and the capillary circulation within the pericardial gland. No note is taken of the extensive series of pallial sinuses connected with the efferent branchial trunk (after Howes).

a. auricle of the heart; *a.ad.* anterior adductor; *a.p.* anterior protractor muscle; *ef.br.v.* efferent branchial veins returning blood to auricle; *ef.br.t.* efferent branchial trunk; *ef.p.v.* efferent pallial veins; *pc.* pericardial chamber; *pl.p.* plexus within pericardial gland; *r.* rectum traversing ventricle; *v.* ventricle of the heart opened to show the rectum and the auricular orifice.

lamellæ, flowing as arterial blood into the efferent branchial arteries, placed along the junction of the secondary limb of the inner gills with the body wall, and also at the junction of the secondary limb of the outer gills with the pallial lobes, where the blood combines with that brought by the efferent pallial vessels from the mantle and proceeds thence to the auricle, either directly or by way of the pericardial gland. Some venous blood, however, passes direct to the branchial arteries or to the auricles without undergoing the portal circulation through the kidneys, and a much larger quantity, which has been purified within the mantle lobes, does not enter either the renal organs or the branchiæ, but, mixed with some from the outer gills, undergoes a portal circulation within the pericardial gland before entering the auricles.

Although the vascular mantle lobes largely assist in the oxygenation of the blood, the respiratory organs are normally constituted by the branchial lamellæ or gills, which arise from a longitudinal vascular

ridge on each side of the body, separated by the foot and known as the right and left ctenidia or branchiæ, according to their position. They are each formed by a pair of trellised and vascular lamellæ, united at the base and each composed of a descending adaxial or primary lamella, which becomes acutely reflected to form an ascending secondary limb, the distal margin of each external gill being fused to and vascularly continuous with the mantle lobe of its side; while the ascending or secondary limbs of the inner gills are similarly fused anteriorly with the visceral body wall, but posteriorly, the secondary limbs of the right and left inner gills fuse together and form the partition or septum separating the branchial and cloacal cavities.

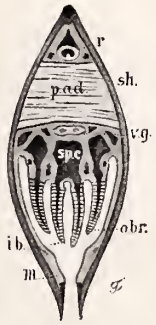


FIG. 346.—Transverse section through the posterior region of *Anodonta cygnea*, immediately behind the foot, to show the arrangement of the organs and the coalition of the supra-branchial chambers of the inner gills, owing to the fusion of the secondary limbs of the right and left inner gills (after Howes).

i.b. inner gill or branchia; *m.* mantle lobes with marginal pallial muscles; *o.br.* outer gill or branchia; *p.ad.* posterior adductor muscle; *r.* rectum, showing typhlosole; *sh.* shell; *sp.c.* combined supra-branchial chamber of the inner gills; *v.g.* visceral or parieto-splanchnic ganglia.

The spaces or cavities between the primary and the secondary lamellæ of each gill are occupied by exuberant sub-filamentar outgrowths, which obliterate the inter-filamentar spaces and bridge over and bind together the opposite sides of the cavity by interlamellar fibrous or vascular junctions, which arise at regular intervals, coincident in position with or forming the larger vertical blood vessels.

The vertical filaments, which were primitively the respiratory organs, have in *Anodonta* lost their original blood-carrying function and become comparatively firm and solid rods supporting the spongy, lacunar and turgescible blood permeated tissue, within which definite blood channels are excavated and respiratory processes carried on. The interlamellar junctions in the

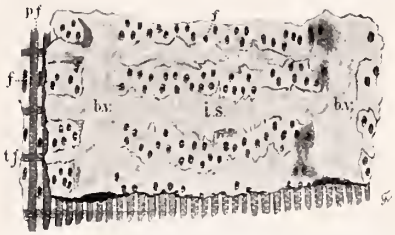


FIG. 347.—Fragment of the outer or primary limb of the inner gill of *Anodonta*, torn from the connected inner or secondary lamella, to expose the constituent filaments and the fenestræ, highly magnified (after Holman Peck).

b.v. large vertical blood vessels; *f.* fenestræ or water passages piercing the interlamellar lacunar outgrowth, *i.s.*; *p.f.* primitive vertical filaments; *t.f.* transverse interfilamentar junctions.

outer gills are long vertical ridges of solid lacunar tissue placed at intervals of about every seventh filament, and supporting a blood vessel at each side. The interlamellar junctions of the inner gills are hollow and vascular, and placed at intervals of about twenty filaments apart, alternating in position on the primary and secondary limbs of the gill.

The transverse filaments are wavy transverse rods crossing the straight vertical filaments at regular intervals, and thus forming a regularly trellised pattern and enclosing vertically oblong interfilamentary spaces, within which are the openings of undulatory rows of minute, irregular and somewhat oblique fenestræ or water passages, varying in size from $\frac{1}{250}$ to $\frac{1}{1000}$ of an inch in diameter, which pass through the subfilamentar lacunar tissue of the gill cavity.

The GLANDULAR system in *Anodonta* is practically identical, in its broad features, with that described in *Helix*, the mantle, and tissues generally, presenting a very glandular structure, the glands being formed of differentiated epithelial cells, with calcareous, pigmented or mucous contents. Lime cells, capable of secreting nacreous or shelly matter, are so plentifully distributed over almost every part of the surface of the animal, that the stimulus or irritation of its delicate tissues by the accidental presence of any extraneous inorganic or organic particles, immediately leads to the formation of pearls or pearly concretions by the concentric deposition around the intruding object, of calcareous substances similar in structure to the inner layer of the shell itself, but varying somewhat in character according to the position in which the intruding particles may have become lodged.

The Nephridia, Renal organs, or organs of Bojanus are symmetrically paired, tubular and sac-like, glandular or excretory organs, which are each folded upon themselves at the posterior end, the ventral or secretory limbs having their walls thrown into thick spongy brown folds, clothed with blackish ciliated epithelium. Each dorsal limb, or Ureter, is a thin-walled tube, very wide posteriorly, whose upper walls are continuous with, and inseparable from, the floor of the pericardium, while its floor is continuous with the roof of the glandular section which it overlays.

The organs are placed side by side beneath the pericardium and in front of the posterior adductor, but, although separated by the Vena-cava or great central blood vessel, the excretory portion or ureter of each kidney is united by a wide inter-renal oval space near the anterior

end, and the two glandular parts are similarly, but more ventrally connected. The secretory limbs are also joined anteriorly to the anterior part of the pericardium by the reno-pericardial funnels, which open within the pericardial cavity by a pair of somewhat crescentic slits.

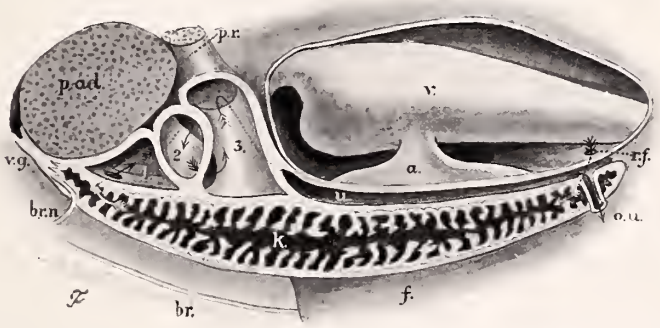


FIG. 348.—Longitudinal section through the right Renal organ or Nephridium of *Anodonta cygnea*, illustrating its relation to the pericardium and also showing its structure and the intricate series of connecting chambers between the glandular section and the ureter × 3 (after Rankin).

a. auricle of the heart; *br.* left branchia; *br.n.* branchial nerve; *f.* foot; *k.* kidney or renal organ of right side laid open; *o.u.* external orifice of right ureter; *p.ad.* posterior adductor; *p.r.* posterior retractor; *r.f.* right reno-pericardial funnel, connecting the pericardium with the glandular part of the kidney; *u.* ureter, showing the three complex chambers intervening between the glandular section; *v.* ventricle of the heart; *v.g.* visceral or parieto-splanchnic ganglia.

The venous blood on its way to the branchiæ from the vena-cava circulates within an intricate renal plexus, the renal cellules during the passage of the blood through the organ eliminating the nitrogenous waste matters in the form of urea, uric acid, etc., which are expelled from the system by the right and left ureters, which terminate in a pair of small outwardly directed orifices with prominent whitish margins, opening respectively into the right and left exhalent chambers and always placed above the cerebro-pleuro-visceral commissure.

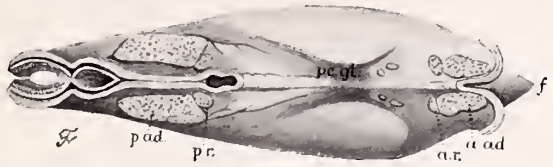


FIG. 349.—Dorsal view of *Anodonta cygnea* to show the position and aspect of the organ of Keber or pericardial gland (after Grobben).

a.ad. anterior adductor; *a.r.* anterior retractor; *f.* foot; *p.ad.* posterior adductor; *p.r.* posterior retractor; *pc.gl.* pericardial gland, the four anteriorly placed symmetrical scars are indications of the anterior umbonal retentor muscles.

The Pericardial Glands or Keber's organs are rusty-red, paired glandular proliferations of the anterior epithelial walls of the pericardium which have an excretory function analogous to that of the

renal organs. They have a rich sanguine irrigation mainly by the arterial blood returning to the auricles from the mantle lobes and outer gills, from which the glands eliminate a still more acrid secretion than that of the nephridia, which is probably discharged into the pericardium and passes outwards by way of the reno-pericardial orifice and the ureter.

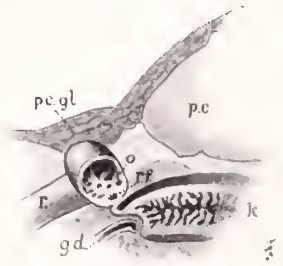


FIG. 350.—Longitudinal section through the right accessory pericardial space of *Anodonta cygnea* to show the openings of the pericardial gland and the reno-pericardial funnel and neighbouring organs × 3 (after Grobben).

g.d. right genital duct; *k.* anterior end of kidney in section, showing its glandular structure and the more dorsally placed ureter; *o.* openings of pericardial gland into the accessory space; *p.c.* pericardium; *pc.gl.* pericardial gland; *r.* rectum; *r.f.* reno-pericardial funnel.

The Lymphatic Glands are, as in *Helix*, diffused amongst the connective tissue in almost all parts of the body, but although the function is more especially concentrated within the gills, it is not localized, and does not form a definite organ as in some of the Opisthobranchs.

The MUSCULAR system of *Anodonta*, so far as relates to the larger and more extrinsic muscles, may be termed Pedal or Pallial, according to the area with which they are most closely identified: there are,

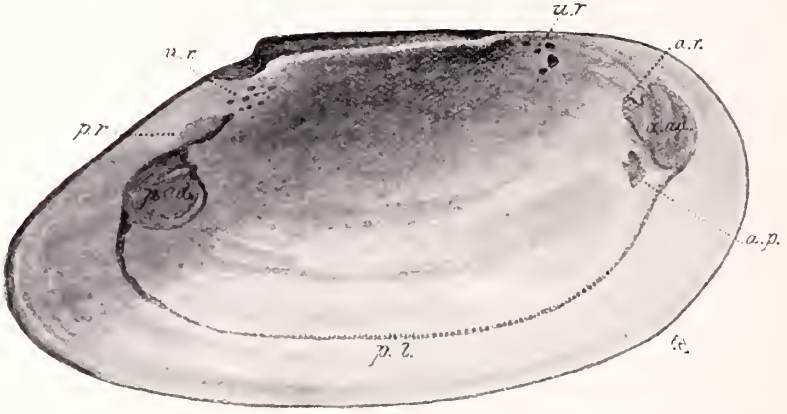


FIG. 351.—The left valve of an *Anodonta cygnea* from Clumber Lake, Notts., collected by Mr. C. T. Musson, F.L.S., showing the muscular scars, which indicate the places of attachment of the extrinsic muscles.

a.ad. anterior adductor scar; *a.p.* anterior pedal protractor scar, the abdominal retentor scar of Clessin; *a.r.* anterior pedal retractor scar; *p.ad.* posterior adductor scar; *p.l.* pallial line; *p.r.* posterior pedal retractor scar; *u.r.* umbonal retentor or pedal levator scars.

however, innumerable smaller, though intrinsic muscles beneath and intimately connected with the general integument, while the walls of

the alimentary canal, the heart, the arteries and other organs are all more or less closely invested with or composed of muscular fibres.

The places of attachment of the extrinsic muscles to the internal surface of the valves is indicated by distinct and permanent scars, owing to the fibres composing the muscles being connected to the epithelial cellules, whose calcified cuticle forms the nacreous lining of the shell.

The Pallial muscles are chiefly developed towards the mantle margin and are composed of variously directed and interlaced muscular fibres, which, however, mainly run in three directions, viz. : parallel to the mantle margin, at right angles to it, or perpendicularly to the two first-named and joining the inner and outer pallial surfaces; those fibres running at right angles to the margin are the most strongly and numerously developed, they are proximally attached to the

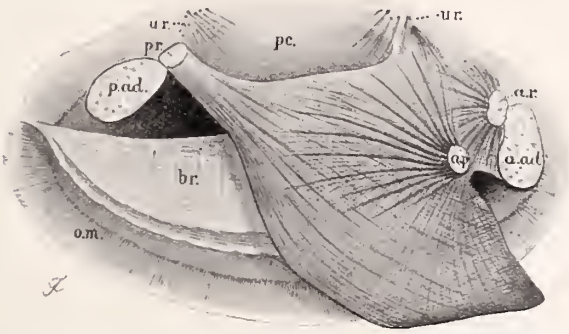


FIG. 352.—Muscular system of *Anodonta fluviatilis*, illustrating the distribution and functional area of the extrinsic muscles. The right mantle lobe and right branchiæ removed (after Simpson).

a.ad. anterior adductor; *a.p.* anterior protractor, showing the radiation of its muscular fibres and their comparatively superficial position; *a.r.* anterior retractor, showing its deeply seated ramifications; *br.* left branchiæ; *o.m.* orbicular muscles, showing their sub-marginal insertion in the shell to form the pallial line, their posterior modification form the siphonal retractors; *p.ad.* posterior adductor; *pc.* pericardium; *p.r.* posterior retractor, the fibres of which are not so superficially distributed generally, as those of the protractor, but less deeply imbedded than those of the anterior retractor; *u.r.* umbonal retentors or pedal levators, distributing their fibres over the region of the stomach, pericardium, etc.

inner lining of the shell and form the retractors of the mantle margin, being distinguished as the Orbicular muscles, their line of attachment to the shell constituting the linear sub-marginal muscular scar, known as the pallial line, which runs parallel with the ventral margin of the shell and is also continuous with the external margin of the adductors.

At the posterior margin of the mantle, these complex and variously divergent muscles become specialized to form the siphonal retractors, the constituent muscular fibres taking a circular, longitudinal or radial direction.

The Adductor muscles are also considered to be a great local development of the pallial muscles, with which they are continuous; in *Anodonta* the adductors are formed by two large, powerful and subequal muscular masses, composed of numerous closely arranged muscle fibres and placed at opposite ends of the body, at about an equal distance from the ligament; they pass perpendicularly through the body of the mollusk between the inner faces of the valves which they unite together and close by their contractions, the anterior adductor being anterior and dorsal to the mouth, while the posterior lies beneath and anterior to the rectum, but they, in common with the extrinsic muscles generally, gradually move with the growth of the shell, diverging and becoming more distant from the hinge and from each other, leaving traces of their former positions by the gradual narrowing and convergence towards the umbones of the scars, which mark their places of prior attachment.

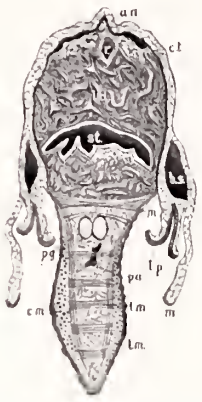


FIG. 353. — Transverse section through anterior region of *Anodonta anatina* showing the arrangement of the foot muscles and the duplicature of mantle (after Vogt and Yung).

a.a. anterior aorta; *b.s.* blood sinus at base of palps; *c.m.* cross muscles seen as cut transversely; *c.t.* connective tissue about digestive gland; *l.d.* ducts of liver or digestive gland; *l.m.* longitudinal pedal muscles; *l.p.* labial palps; *m.* muscles between foot and body; *p.a.* pedal artery; *p.g.* pedal ganglia; *r.* rectum; *st.* stomach; *t.m.* transverse pedal muscles.

The Pedal muscles are paired symmetrically, and formed by the retractor, protractor, and levator or retentor muscles, which are all proximally attached to corresponding positions on the inner surfaces of each valve, on which they leave distinct impressions or scars; distally they mainly terminate amidst the intrinsic musculature and tissues of the foot.

The Anterior protractors are muscular masses formed by radiately divergent muscle fibres, which assist in the protrusion of the foot and are spread over and superficially attached to the surface of the foot and proximally inserted on each valve, a short distance from and posterior to the anterior adductor.

The Anterior retractors, at their origin, are often continuous postero-dorsally with the neighbouring adductor, they penetrate deeply within the tissues of the foot, and for the most part are more deeply imbedded than the fibres from the posterior retractors; they

are more especially distributed along the anterior margin, some of the fibres being also dorsally spread over the region of the liver.

The Posterior retractors are situate dorsally to, but contiguous with the posterior adductor, and originate as firm muscular trunks ; the fibres into which they are divided become more especially distributed about the lower part of the body and along the free ventral edge of the foot, and, though generally more deeply placed, are often closely intermingled with the more superficially placed protractor fibres.

The Umbonal retentor or Levator muscles are, in *Anodonta*, formed by one or more groups of more or less isolated fibres fixed near to or within the umbonal area, their fibres spreading over the region of the stomach and of the pericardium. Many of the fibres do not, however, reach the shell, their proximal extremities calcifying beneath the mantle.

The Intrinsic Pedal muscles are very numerous and intricate and formed by a complex arrangement of variously directed and interlacing muscle fibres, the longitudinal ones being continuous with or connected to the great retractors of the foot, while the transverse muscle bundles and the more superficially placed layer of circular fibres assist in its contraction and protrusion.

The Reproductive organs of *Anodonta* are normally of a diœcious character, the two sexes being developed in different individuals, although hermaphrodite specimens are sometimes found.

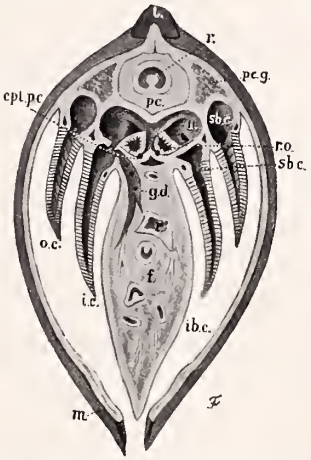


Fig. 354.—Transverse section through the anterior part of the pericardium of *Anodonta cygnea* to show the position of the genital and nephridial ducts and their relation to the supra-branchial chambers of the inner gills (after Howes).

c.pl-p.c. cerebro - pleuro - visceral commissure, with the Vena cava beneath ; *f.* foot, with contained genital glands and showing cross sections of the intestinal tract and more longitudinal ones of the subsidiary genital ducts ; *g.d.* genital duct of left side opened up to show outlet ; *i.c.* inner ctenidium, the left showing the outlet of the genital and renal ducts ; *ib.c.* infra-branchial chamber ; *l.* ligament of shell ; *m.* mantle lobes lining shell and showing marginal pallial muscles ; *o.c.* outer ctenidium ; *pc.* pericardium ; *pc.g.* pericardial gland or organ of Keber ; *r.* rectum with typhlosole ; *r.o.* renal organ, glandular portion, showing beneath the more dorsal efferent renal chamber or ureter ; *sb.c.* supra-branchial chamber ; *u.* the left ureter showing the opening into the supra-branchial chamber of the inner gill.

The genital glands are very voluminous, symmetrically paired, and placed at either side of the body, occupying the upper part of the

visceral mass, above the muscular part of the foot and investing the convolutions of the intestinal tract; they are however of the simplest and most primitive character and very similar in both sexes, although the male gonad can often be recognised by its whitish colour, without microscopic examination.

Each gland or gonad is formed by an immense aggregation of richly branched and minute racemose lobules, scarcely half-a-millimetre in diameter, the ducts from which unite to form a short common duct from each gland, which opens by a minute aperture close by the ureter into the cavity of the inner gill within the supra-branchial chamber of its side.

FIG. 355.—A Lobule of the genital gland of *Anodonta anatina*, with its efferent duct, and showing the developing ova, highly magnified (after Vogt and Yung).

There are no accessory organs developed in connection with the reproductive system, and sexual congress is therefore impossible, and necessitates the social aggregation of these mollusks within limited areas to ensure the fertilization of the ova, as the spermatozoa are simply and freely discharged into the surrounding water with the exhalent current by the male, and drawn with the inhalent water by the branchial siphon into the pallial cavity of the female, probably fertilizing the ova while within the gill lamellæ.

Although, in the foregoing pages, I have briefly examined examples of a typical Gastropod and Pelecypod, chiefly from a morphological standpoint, yet the various species of our fauna, owing to the specialization of habits or function they have undergone, exhibit such modifications of their various organs that this phase of our study would be incomplete without a fuller account of the organs individually, detailing the differentiations in structure and function they each undergo, and referring to the phylogenetic and other points of interest in connection therewith. For this purpose I propose to adhere to the method I have hitherto followed of first treating upon the external features and afterwards studying the internal organization.

The Morphology of the External Organs.

THE HEAD AND ITS ORGANS.

The Cephalic region, which in both Gastropods and Pelecypods may be distinguished as the Prosoma, is bilaterally symmetrical, and arises in the embryo from the upper surface of the Velar area, the size of which, according to Gegenbaur, is correlated with the differentiation of the head. In the adult this region is indicated by the position of the oral orifice, and in the Gastropoda is formed by the distinct and usually well-developed, somewhat cylindrical head and its appendages, placed at the anterior end of the body, and borne by a more or less evident and intervening constriction or neck, on the right side of which is placed the common genital orifice, or, as in the Streptoneures, may bear the muscular and non-invaginable male organ. The whole cephalic region is usually capable of being protruded beyond and completely withdrawn beneath the mantle for protection.

Fig. 356. — Head and Tentacles of a Gastropod, *Helix aspersa* × 2.

In the Pelecypoda the distinct head of the assumed ancestor has become atrophied and lost, and there is therefore no specialized or perceptible head, its position being now only indicated outwardly by the transversely oval mouth, with its encompassing lips and palps.

The Mouth, or oral aperture with its labial appendages, is situated on the ventral surface of the head, or may, as in Streptoneures, be placed at the extremity of a long and contractile rostrum. It originates, during the development of the embryo, as a simple invagination of the ectoderm, termed the Stomodæum, which meets and joins with the mesenteron or mid-gut. In those cases where the blastopore or orifice of primitive invagination remains permanently open to form the mouth, a prominence or wall becomes developed which surrounds or encompasses it.

Fig. 357. — Mouth of *Arion ater* × 10 (after Moquin-Tandon), showing also the jaw, the upper and lower lips, and the lobulate organs of Semper on the upper lip.

In the mollusca, as in other Invertebrates, the mouth is only fitted for the inception of food, the respiratory orifice, which in some of the higher animals is in a measure confounded with the oral opening, being quite removed from its proximity.

The Muzzle or Prostomium is the region anterior to the base of the tentacles and projecting in front of the mouth; it is the essential part of the head, and intimately connected with the power of forward locomotion in a definite direction and with the general orientation or carriage of the body, and, in the Gastropoda, is generally short, somewhat convex and angulated at each side, while its attenuate anterior margin was distinguished by Draparnaud as the Chaperon or Hood. This feature is very perceptible in the species of the family *Limnæidæ*.

Fig. 358.— Ventral aspect of *Limnæa stagnalis* var. *fragilis* showing the mouth and the attenuate anterior margin of the head, known as the Chaperon or Hood.

The muzzle may, however, as in *Cyclostoma*, be produced into an elongated and somewhat annulate pre-oral structure or Rostrum, of a more or less cylindrical shape, sometimes dilated or slightly cleft at its distal extremity, which possesses lips and other oral organs, and is susceptible of a considerable amount of elongation and contraction, but not being a retractile organ it cannot be withdrawn within the body cavity, although its parts are so strongly contractile, that when contraction takes place, the mouth is so drawn in as to lie at the bottom of a distinct depression.

Fig. 359.–Ventral aspect of the contracted rostrum of *Cyclostoma elegans* × 4 (after Simroth).

None of our native species possess the introvertible or truly retractile Proboscis, which seems more particularly to characterize the carnivorous Streptoneures.

In the Pelecypoda, the portion of the body anterior to the mouth, which embraces the region of the anterior adductor, may be regarded as representing the Prostomium.

The Facial Grooves are an extension of the symmetrically arranged yet intricate plexus of channels distributing the mucus over the body, and show upon the face or muzzle, in some species, as two little central and parallel longitudinal channels, which are prolongations of the dorsal grooves and variously ramify over the anterior surface of the muzzle.

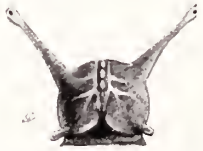


Fig. 360. — Facial Grooves of *Amalia sowerbyi* × 2.

In *Amalia sowerbyi* the two dorsal channels clearly show upon the forehead, and each usually throws off outwardly a delicate branch

towards the base of the ommatophore of its side, both main channels afterwards becoming rather regularly trifid before their final obliteration. In *Limax maximus* these light coloured grooves or mucus channels are much simpler in character, each dorsal furrow merely giving off one slender branch towards the ommatophore of its side. All our Gastropoda do not, however, possess these distinctly defined ramified channels, as I have been quite unable to detect recognizable indications of their presence in many species.

The CEPHALIC TENTACLES, which arise during larval development from the area encircled by the velum, are pre-eminently sensitive, tactile and symmetrically paired processes of the body wall, and are always innervated by the cephalic ganglia, and placed on the antero-dorsal aspect of the animal. They are the most noticeable and prominent appendages of the cephalic region, being very mobile and possessing a considerable variety and range of motion, and externally covered in the terrestrial species with fine granulations or annular ridges, and in the aquatic species with a very noticeable vibratile epithelium.

They may be divided, according to their structure, into two groups, viz.: Retractile and Contractile. The retractile tentacles are hollow and muscular cylindrical processes, each terminated by a bulbous enlargement, and capable of being withdrawn within the body of the animal and are more especially a characteristic of the terrestrial species. The contractile tentacles, for which Ehrenberg proposed the term Vibracles to distinguish them from the retractile tentacles of the Helices, are solid, homogeneous and projecting cephalic processes, only capable of shrinkage or contraction, and are quite incapable of being withdrawn within the body cavity like the retractile tentacles of the Stylommatophores.

The Stylommatophores have usually two pairs of elongate, cylindrical and tapering hollow tentacles, which are filled with blood and connected with the blood spaces of the head, and bear a well-developed bulbous distal extremity. The dorsal or posterior pair, in addition to olfactory organs, bear the eyes at the bulbous end, being hence termed Ommatophores or eye-bearers, and are usually three or four times longer than the anterior pair, which, however, are very similar in general organization. The anterior tentacles, however, vary greatly in their development; in *Buliminus* and *Pupa* they are very short, and in *Carychium* quite rudimentary, while in *Vertigo* no external trace of their existence can be detected.

Both pairs are exceedingly flexible and can, at the will of the animal, be withdrawn for safety within the body cavity by the contraction of the special retractor muscle, fixed to the apex of each tentacle, a mode of retraction termed Acrembolic by Prof. Ray Lankester; their eversion and also elongation being accomplished by blood pressure and the successive or wave-like contraction of the annular or transverse muscular fibres of the organ, the apex or bulbous end being the last part protruded: this method of eversion or unfolding by the sides has been distinguished by the term Pleurecbolic, in con-

Fig. 361. Fig. 362. Fig. 363. Fig. 364.

Retractile tentacles of a Stylommatophore, showing the retractor muscle and illustrating the various stages of the mode of retraction and eversion, termed Acrembolism and Pleurecbolism. The figures viewed from left to right show the tentacle in process of retraction and from right to left as undergoing extension or protrusion.

Fig. 361 shows the tentacle completely extended; Fig. 364 completely invaginated; Figs. 362 and 363 illustrating the intermediate stages.

tradistinction to the terms Acrecbolic and Pleurembolic, which distinguish the processes by which the introvertible or retractile probosces of some Streptoneures are protruded and retracted.

The Streptoneura of our fauna have only two well-developed tentacles, which may be comparatively thick and rounded at the extremity, as in *Cyclostoma elegans*, or extremely long and delicately tapering to a fine point, as in *Bythinia tentaculata*, which receives its specific name from the length and delicacy of its tentacles, but both forms are contractile only, and cannot be retracted or drawn within the body cavity for protection, as can the hollow retractile tentacles of the Stylommatophora. Although, in the terrestrial species of Streptoneura, an organ of olfaction may be located near the apex of each tentacle, as in the Stylommatophora, yet the eyes are placed on short pedicels behind, which are more or less intimately fused or combined with the more developed tactile tentacles.

Fig. 365.—Dorsal aspect of the cephalic region of *Cyclostoma elegans*, showing the contractile tentacles × 4 (after Moquin-Tandon).

The right tentacle of the male in some groups, as in the *Viviparæ*, is noticeably stouter than the left, this sexual dimorphism being due

to its containing the male organ of reproduction, the tentacle being perforate at the apex for its protrusion, but when not located within the tentacle, this organ may be placed as a non-invaginable projecting

FIG. 366.—Head of *Vivipara vivipara* ♂ to show the malformed right tentacle, due to containing the male organ of reproduction (after Simroth).

FIG. 367.—*Valvata piscinalis* showing the large non-invaginable male organ on the right side of the neck (after Moquin-Tandon).

process of the body wall, behind it, upon the right side of the neck and there simulate a third tentacle, as in the *Valvatidæ*.

The two tentacles of the Basommatophora are also contractile only and are elongately subulate or flatly triangular processes, according to the genus, the right tentacle being often distinctly broader basally than the left; the whole surface is covered with fine, transparent and very sensitive vibratile cilia, which have a very vigorous rhythmical movement, producing perceptible currents in the surrounding water, as is evidenced by the attraction or repulsion of small floating particles, according as they have become involved in the approaching or departing current. This action is always most striking when the animal is in motion with its tentacles extended, becoming weak and languid if the tentacles are contracted or the animal be injured or sickly. In *Ancylus fluviatilis* the cilia of the tentacle continue in motion for nearly a hour after the excision of the tentacle from the head, the gyrations it performs recalling the rotation of the embryo, which is also caused by cilial action.

FIG. 368.—Head of *Planorbis marginatus*, showing the contractile and slender subulate tentacles, × 10.

FIG. 369.—Head of *Limnæa stagnalis*, showing the characteristic thin, triangular and contractile tentacles.

The LABIAL PALPS or lobes in Gastropods are, when distinctly developed, exceedingly mobile processes around the mouth, capable of a considerable amount of extension and contraction, and delicately sensitive to tactile impressions, receiving their innervation from the cerebral ganglia, and preserved in a moist and sensitive condition by

the special mucous secretions from the unicellular glands of the organ of Semper; they represent the largely developed bilobed velum of larval life and are retained in the *Limnæidæ* in full proportions by the adult, but have lost the marginal fringe of relatively very long cilia and also the locomotor function.

Some authors distinguish three circum-oral lobes in the Gastropods, an upper lip which is somewhat rounded and often bears a number of papillæ, and two lateral ones, which however are usually regarded as representing a cleft lower lip.

Fig. 370. — Mouth of *Helix aspersa* × 4, showing the lateral lobes or lips and upper jaw (after Howes).

These processes are not retractile like the ommatophores and are chiefly found in the predacious species, but are also largely developed in the *Limnæidæ*, forming a considerable circum-oral expansion or enlargement, but in a less pronounced form these labial lobes are present in other pulmonates. In *Limax*, *Arion*, etc., the upper lip bears a number of distinct and rounded tubercles or papillæ, into which the glands of Semper's organ debouch (see p. 185, f. 357), and which are innervated by a branch from each of the anterior tentacular nerves, which gives off to each papilla of its side a nervous branch upon which a small ganglion is developed.

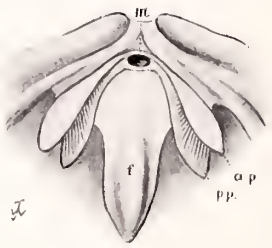


Fig. 371. — Anterior region of *Anodonta cygnea*, showing the position of the mouth and the relative disposition of the labial lobes and foot (after Moquin-Tandon).

a.p. right anterior palp ; *f.* foot ; *p.p.* right posterior palp ; *m.* mouth.

The labial palps are, however, a more especial feature of the Pelecypods. They consist of two pairs of triangularly-oval, thin and highly vascular processes, innervated by the cerebro-pleural ganglia and covered with richly ciliated epithelium. They are formed by the excessive prolongation and out-growth of the anterior and posterior margins of the oral aperture and hang down within the mantle cavity, enclosing between them a ciliated groove conducting directly to the mouth the particles of food brought within the influence of the currents which the action of the cilia perpetually excite, and are therefore more especially alimentary and respiratory in function rather than of a tactile or sensory character.

Fig. 372.—Anterior and posterior labial palps from the right side of *Anodonta cygnea*, isolated, × 3 (after Moquin-Tandon).

Though a very constant characteristic of the Pelecypoda, they are apparently quite absent in some few marine genera, but in others are so greatly developed as to be even larger than the branchiæ; they have been termed the lesser and the accessory branchiæ by Swammerdam and other authors, as their great vascularity and position, each in connection with a large pallial sinus, suggests some connection with the respiratory function, their ctenidiform appearance being materially increased by the presence of numerous transverse folds or ridges, which are most pronounced towards the distal margin, becoming less distinct or even deficient as the base of attachment is approached. These transverse ridges also vary considerably in number and relative size, according to the species, those of *Unio* being proportionately larger than those of *Anodonta*, and much more so than *Dreissensia*, in which there are thirty-five of these ridges on each palp, six times finer than the branchial filaments In *Anodonta* there are sixty-five ridges on each palp, while in *Sphærium corneum* var. *nucleus* there are only twelve.

FIG. 373.—Three ridges of the labial palps of *Anodonta cygnea*, to show the arterial vessels, highly magnified (after Keferstein).

FIG. 374. — Four ridges of the labial palps of *Anodonta cygnea* highly magnified (after Moquin-Tandon).

The bases of the palps are practically almost joined to and continuous with the lines of attachment of the gill-lamellæ, the anterior palps being apparently continuous or coterminous with the outer gill-laminæ and the posterior palps being similarly continuous with the line of attachment of the inner branchiæ, leading Prof. Lankester to suggest that the branchiæ and labial palps may be modifications of a double horse-shoe shaped area of ciliated filamentous processes which existed in the more primitive mollusk.

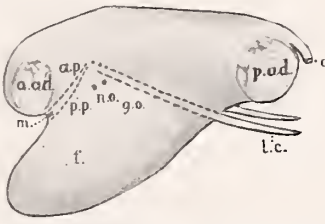


FIG. 375. — *Anodonta cygnea*, with the palps and gill-lamellæ removed to show the apparent continuity of the labial palps and the gills (after Lankester).

a. anus; *a.ad.* anterior adductor; *a.p.* line of attachment of anterior palp, practically continuous with line of attachment of outer gill; *f.* foot; *g.o.* left ureter; *l.c.* axis of the left ctenidium or gill, showing lines of attachment of inner and outer gills; *m.* mouth; *n.o.* orifice of left reproductive gland; *p.ad.* posterior adductor; *p.p.* line of attachment of posterior palp, practically continuous with line of attachment of inner gill.

THE PEDAL OR VENTRAL REGION.

The Podium or foot, which arises during development as a prominence between the mouth and the anus, is the most persistent and characteristic molluscan organ, and is formed by an excessive development and specialization of the cellular and unstriated somatic musculature of the ventral surface of the body, in adaptation to a creeping mode of life, receiving its innervation from special nervous enlargements called the pedal ganglia. The whole surface contains innumerable unicellular mucous glands, and, in addition, there are important and extensive aggregations of similar cells situate in certain definite parts, which render probable a morphological connection between the glands of the Pelecypoda and those of the Gastropoda.

In Gastropods the foot, though varying greatly in size and shape, usually presents a long and broad plantar surface or sole, which occupies the whole ventral surface of the body, but those species with narrow plantar area are apparently endowed with more rapid locomotive powers than those with a more expanded surface. In the aquatic species the surface of the foot is richly covered with vibratile cilia, but in those of terrestrial habit the ciliated area is comparatively restricted.

Fig. 376.—Ventral aspect of the foot of *Helix aspersa*, showing its character and general form, as seen crawling up a slip of glass (from an instantaneous photograph).

The Peripodial Groove or pedal furrow is a more or less distinctly marked groove, separating the body region from the sole and is more especially found in the nude species; it runs parallel with the edge of the sole of the foot along its whole length round the body, and is occupied by a more or less conspicuous row of narrow, oblong, horizontal tubercles, upon which the tubercles of the sides of the body rest uncomformably. The groove in some genera rises slightly towards the tail, where there is often a Caudal mucous gland containing a greater development and concentration of

Fig. 377. — Peripodial Groove and Foot Fringe of *Arion ater* × 2.

fr. foot fringe; *p.f.* peripodial groove or pedal furrow.

mucous cells. The super-families, Aulacopoda and Holopoda, are based upon the presence or absence respectively of the pedal grooves, which, when present, are ventrally circumscribed by the Foot Fringe, a feature distinctly present in some forms and constituting the lateral border of the foot. In *Arion* it is often very brightly and vividly coloured, and variegated at regular intervals by numerous dusky and black, alternately placed, vertical lineoles, which in strongly coloured individuals may be continued across the side areas of the sole. As the tail is approached these lineoles become placed nearer together and more obliquely directed.

The foot, in some groups, gives off various lobes or processes, which when arising from the Epipodium, a thickened ridge along the upper margin of the sole, are known as Epipodia; the Operculigerous lobe of the Streptoneures, which secretes the operculum, is a dependence of the hinder portion of this epipodial ridge, while the Cephalic lobes of *Vivipara* are a development of the anterior part, such processes being distinguished from cephalic tentacles by receiving their innervation from the pedal or pleural and not from the cerebral ganglia.

Fig. 378.—Prosoma of *Vivipara vivipara* ♀ (after Moquin-Tandon), to show the epipodial Cephalic lobes.

Analogous processes, termed Parapodia, may, however, originate along the basal edge of the sole; such outgrowths, though highly developed in many Opisthobranchs, are not noticeably present in our

Fig. 379.

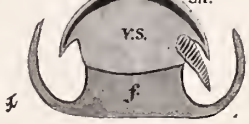


Fig. 380.

Diagrammatic sections through the body of a Streptoneurous and of a Tectibranchiate Gastropod, showing the relative positions of the Epipodial and Parapodial lobes (after Lang).

Fig. 379.—A Streptoneure; *f.* foot, with epipodial lobes; *sh.* shell; *v.s.* visceral or body cavity.
Fig. 380.—A Tectibranch; *f.* foot, with parapodial lobes; *sh.* shell; *v.s.* visceral sac with ctenidium.

land and freshwater species, although the spreading sides of the foot of *Helix pomatia* may be regarded as incipient parapodia.

In certain extra-British species, the primitively sole-shaped foot has, by adaptation to special modes of life, lost its original form and by transverse constrictions, become formed into three regions, termed the Propodium, the Mesopodium, and the Metapodium, which respec-

tively indicate its anterior, middle, and posterior regions, yet in our native species, with the exception of *Acicula*, which, according to Dr. Gray, has a transversely divided sole like *Truncatella*, these parts are so intimately blended together that we are only able to distinguish the metapodium owing to its being indicated by the operculum on its upper surface.

Though not divided transversely, the sole may have well marked longitudinal divisions, and this feature is carried to the greatest extent in *Cyclostoma elegans*, in which species the foot is medially cleft and separated along its whole length, each part being advanced alternately during locomotion. In *Valvata piscinalis* and *V. cristata* this cleavage is confined to the prolonged anterior part of the foot, where the divided parts become widely separated and divergent, simulating a pair of podial tentacles. In our native species of *Viviparа*, although the anterior portion of the foot is similarly prolonged beyond the muzzle, it is not medially cleft, so that the creature is said to be prevented from feeding except when at rest.

FIG. 381. — *Cyclostoma elegans*, showing the longitudinally cleft foot, with the right segment in use, the left being contracted and raised, × 2 (after Simroth).

FIG. 382. — *Valvata piscinalis*, showing the cleft and divergent anterior ends of the foot, × 2.

In *Limax*, *Arion*, etc., the sole is more or less distinctly longitudinally tripartite, the side areas being usually more darkly and distinctly pigmented than the locomotory mid area, owing to the thickening of the epithelial and sub-epithelial musculature which

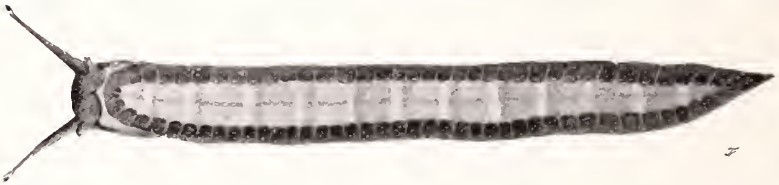


FIG. 383.—Sole of *Limax cinereo-niger*, showing the trifasciate foot and the muscular waves of the mid area, visible during movement (after Simroth).

prevents its free pigmentation. The side and mid areas in *Limax*, though not in *Arion*, are also separated by more or less distinct longitudinal furrows, which, though often imperceptible during life, become visible after the immersion of the animal in boiling water or alcohol ; but in the testaceous Euthyneures the entire sole is more or less

locomotory and muscular, being apparently homogeneous in structure although the mode of pigmentation is not uniform, even in closely allied species. In *Helix aspersa* trifasciation is perceptible owing to the greater pigmentation of the side areas, but in *Helix pomatia* the mid area is the most darkly coloured, the sides being usually quite unpigmented and very distinctly defined thereby.

In the Pelecypods the foot arises ventrally from the body, and in *Nucula* and other archaic species forms a flat sole or creeping disc, by the expansion of the deep longitudinal cleft therein; such forms are distinguished as Reptary, and present a curious similarity to *Helix pomatia* and certain other species, in which the foot is longitudinally folded up in the same manner when the animal is retiring within its shell.

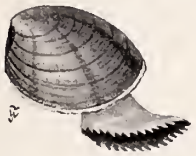


FIG. 384.–*Nucula nucleus* (L.) (after H. & A. Adams), showing the longitudinally grooved or primitive Reptary foot.

Most of our species are, however, Subreptatory, possessing a laterally compressed, very extensile and flexible linguiform or axe-shaped organ, with annular muscular bands to assist in its extension and longitudinal muscles for its retraction, being, however, still expansible as a flattened crawling disc, although the longitudinal groove characterizing the primitive Reptary foot has become lost. The degree of development is in correlation with the habits and locomotory powers of the mollusk, as it may be modified to form an efficient burrowing organ and tend to assume a more anterior position or become somewhat digitiform and vestigial, as in *Dreissensia*. The tip is often more deeply coloured and of a reddish tint, owing to the presence of Tetronerythrine, a substance which corresponds with the hæmoglobin of *Planorbis* and the higher animals and serves for cutaneous respiration by its great affinity for oxygen.

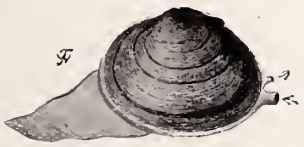


FIG. 385. — *Sphærium rivicola* (Leach), showing the Subreptatory burrowing or crawling foot.

FIG. 386.—*Dreissensia polymorpha* (Pall.), Canal, Northampton, Collected by Mr. L. E. Adams, B.A., Showing the digitiform and vestigial foot.

The tissue of the protruded foot becomes rapidly firm and rigid by blood pressure or, as some believe, by inception of the surrounding

water within a system of vessels which may or may not communicate with the circulatory blood system; the orifices supposed to be aquiferous are, however, merely the outlets of aggregated mucous glands or the vestigial opening of the byssogenous gland which are all placed on the posterior side of the foot. In *Natica josephina*, a marine Gastropod, it has, however, been fully established that, quite independently of the blood system, the foot does contain a very complex and extensive water vascular system, by means of which the foot can be very rapidly expanded and extended for locomotion.

The surface of the foot is richly ciliated and furnished with a great number of unicellular mucous glands, but there are also distinct invaginations of the ectoderm or integument, known as Pedal glands, where mucous cells are aggregated together and distinctly localized.

An Anterior Pedal Gland is possessed by the active aquatic Streptoneures, which opens at the anterior end of the foot by a transverse groove and secretes mucus for the lubrication of the foot and to aid in the process of crawling. This gland is represented in the Pulmonates and in terrestrial Streptoneures by the Supra-Pedal gland, known also as the sinus of Kleeburg, a long epithelial tube with ciliated ventral surface, placed between the muzzle and the foot, which was formerly thought to be an olfactory organ, but which serves as a reservoir and duct for the mucus which its investing cells abundantly secrete. In *Cyclostoma* this gland becomes bifid posteriorly in harmony with the longitudinally divided foot.

FIG. 387.—Prosoma of Helix × 2, showing the position of the Supra-Pedal Gland, *p.gl.*

FIG. 388.—Supra-Pedal Gland of *Cyclostoma elegans* (after Simroth), highly magnified, showing the bifid posterior prolongations.

The Ventral Pedal Sinus is found in *Cyclostoma* and many Streptoneures, being comparable with the byssal cavity of the Pelecypods. It opens on the anterior portion of the foot-sole, forming the aperture of the sole gland, whose glandular epithelial

walls project into the lumen of the body, as a multitude of ramifying tubules and follicles.

The Caudal glands are often found in terrestrial Gastropods at the upper surface of the posterior end of the body, and form a sinus or cavity, such as is present in *Hyalinia* and very conspicuous in *Arion*. In the foreign genera the gland is sometimes distinguished by the development of a more or less striking protuberance. Its secretious, which are very abundant and much denser than those from the skin, accumulate in the more or less triangular caudal cavity.

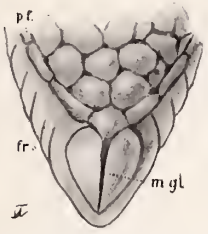


FIG. 389.—The posterior dorsal aspect of *Hyalinia cellaria*, contracted after scalding, to show the Caudal Mucus cavity, and incidentally the rugosities of the body, the fringe and the peripodial groove, × 16.

fr. fringe; *m.gl.* caudal mucous gland; *p.f.* peripodial furrow.

The Pelecypods sometimes possess on the posterior median line an orifice which is homologous with the Ventral pedal sinus of the Gastropods, and communicates with a byssal cavity in which are gathered the secretions of the foot glands, which have permeated the epithelial cellules lining the byssal cavity, and harden on exposure in elastic adhesive filaments, whose aggregation forms the byssus and serves to attach the animal, as in *Dreissensia*. The byssal gland varies greatly in development in different genera and is often present in the young stage when absent in the adult. The calcareous plug of *Anomia* is a modified byssus.

In addition, there are in some species two other glandular orifices, one anterior and the other posterior to the position occupied by the vestigial byssal aperture, which it is possible may represent the anterior and posterior mucous glands of the Gastropoda.

Although mucus is emitted from all parts of the body, that secreted by the Supra-Pedal gland is of the greatest consistency, and in the nude species especially, is exuded so plentifully as to leave an iridescent silvery or tinted mucous trail which marks the course the animal has travelled. This mucus hardens very quickly on exposure to air or water, becoming very tenacious and firm, and is utilized by some species as a means of locomotion and for descent from or ascent to an elevated position.

The Pallial Region.

The Mantle, or Pallium, is a thin and vascular fold of the integument, which is fused to and covers the dorsum of the body and arises during development around the primitive shell gland, its thickened and glandular margins, which are the active formative organs of the shell, enclosing, in conjunction with the body wall, a pallial cavity communicating more or less freely with the external medium and protecting the respiratory organs, which may exist as gills or ctenidia for the respiration of water or, in the terrestrial species, may take the form of a lung constituted by an intricate network of blood vessels distributed upon the roof of the pallial cavity. In the Streptoneures and the more primitive Pelecypods large Hypobranchial mucous glands are developed within the pallial cavity between the rectum and the branchiæ.

The Fusion of the pallial margins to each other and to the body wall to form an enclosed respiratory cavity, has not been carried to a great extent amongst the Streptoneures of our fauna, the cavity being more or less freely open anteriorly to the inhabited medium.

In the Euthyneures this process has, however, become further advanced, and the pallial margins have fused with the body wall, leaving only a small contractile lateral orifice for respiratory and excretory purposes, which divides the mantle more or less distinctly into an anterior and a posterior lobe (see p. 144, f. 304).

In the Pelecypoda the mantle is equally developed laterally, enclosing a symmetrical pallial cavity. In the more archaic forms, as

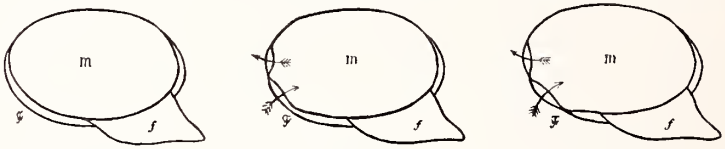


Fig. 390. Fig. 391. Fig. 392.

Diagrams illustrating the position and mode of fusion of the mantle lobes of the Pelecypoda (after Lang). The arrows indicate the direction of the currents. *m*. right mantle lobe ; *f*. foot.

Fig. 390.—Illustrating the primitively open mantle with unseparated respiratory currents.

Fig. 391.—A Biforate Pelecypod, showing a single point of fusion of the right and left mantle lobes, and separating the inhalent and exhalent currents.

Fig. 392.—A Triforate Pelecypod, showing two points of fusion, which form the exhalent and inhalent orifices and a large pedal aperture.

Nucula or *Trigonia*, the pallial margins are quite free ventrally, no provision being made, except such as is provided by cilial action, for the separation of the pure incoming and the impure out-flowing currents. Specialization is evidenced by a vascular fusion of the mantle margins, primarily to ensure the separation of the in-flowing

and out-flowing streams, as this fusion almost invariably takes place near the middle of the posterior margin and cuts off from the great ventral cleft a small exhalent postero-dorsal orifice, directly opposite to the anus; the species with this single point of fusion, which thus divides the great mantle opening into two apertures, a large antero-ventral pedo-branchial cleft and a smaller dorso-posterior anal opening, are termed Biforate. The Naiads illustrate this stage of specialization, although the anal cleft is divided by a central subsidiary fusion into two distinct though connected orifices.

The succeeding stage is characterized by a second point of fusion of the mantle margin, which invariably takes place at a point more ventral than the first and near the junction of the ventral and posterior margins, separating the great pedo-branchial cleft into a branchial and a pedal opening, the anterior one serving for the protrusion of the foot, and the posterior one, which adjoins the anal pallial opening, forming the branchial or inhalent aperture; there are thus three openings, which subserve three distinct functions: such forms are known as Triforate.

This process of fusion is carried to a still further extent in species not within the scope of our studies, both by more points of concrescence and by their greater extent.

The Prolongation of the respiratory apertures to form retractile siphons is a further and extreme specialization of the fusion of the mantle margins, and appears to be a characteristic of an aquatic existence, being strikingly developed among the carnivorous marine Streptoneures. Amongst our species this feature is not noticeably developed, although in *Vivipara* the right cephalic lobe, which is an outgrowth of the foot, becomes folded and forms a siphon which conducts the respiratory water to the branchial cavity.

Fig. 393.—*Limnæa stagnalis* var. *fragilis* (L.), Chislehurst, Kent, collected by Mr. S. C. Cockerell, showing the respiratory aperture contracted.

Fig. 394.—*Limnæa peregra* (Müll.), Christchurch, Hants., showing the prolongation of the pulmonary aperture as a respiratory tube.

Amongst the Basommatophora the *Limnææ* especially are capable

of forming the pallial margin of the respiratory orifice into a long, conical and extensile tube, the delicately sensitive apical orifice of which is kept closed until it reaches the surface of the water, when it is opened to the air for respiratory purposes.

In the Pelecypoda the development of the branchial and anal orifices to form elongate siphons is apparently one of the modifications more especially fitting the mollusk for fluviatile or estuarine life but is more palpably correlated with the habit of burrowing deeply in the muddy or sandy bed of the water they inhabit, and where this peculiar habit of concealment is carried out to the greatest extent the longest siphons are developed, and the constant and regular stream of water necessary for respiratory and alimentary purposes is only able to enter and leave the pallial cavity by means of the elongate siphons, whose protractile orifices project into the water above the place of concealment of the animal ; while in those species which

FIG. 395. — *Pisidium amnicum* (Müll.) × 2, illustrating the development of a single siphon.
Kettering, collected by Mr. C. E. Wright.

FIG. 396.—*Sphærium corneum* (L.) × 2, illustrating the development of two distinct siphonal tubes.
Kettering, collected by Mr. C. E. Wright.

live or move freely in the water, the mantle is usually completely open with respiratory apertures very slightly or not at all prolonged and the papillæ, tentacles and other protuberances more or less sensory in character are distributed indiscriminately along all the free mantle margin. In the burrowing forms these accessory sensory organs are more or less concentrated at the posterior margin, around the siphonal apertures, but more especially at the branchial or inhalent opening.

These prolonged muscular tubes or siphons, which are mostly protruded by blood pressure and withdrawn by the contraction of the modified orbicular muscles, are often separated and form two outwardly distinct channels, as in *Sphærium*, but are very variable in their relative length; in *Dreissensia* and *Sphærium* the branchial siphon is longer than the anal one; but in *Pisidium* the reverse is very strikingly shown, as although the anal siphon is greatly prolonged, the branchial aperture remains unseparated and undifferentiated from the great mantle cleft.

The Extension or outgrowth of the mantle margins may, as in the Euthyneura, form the Auriform Lobe, known as the respiratory and also as the fæcal lobe, a tegumentary appendage near the respiratory orifice, which may bear the anus or termination of the rectum. In *Planorbis* this lobe is largely developed and exsertile with a rich vascularization, and a similar but much smaller and slightly twisted prominence has been observed to exist in certain species of the Helicidæ. The "balancier" of *Vitrina* is a somewhat spatulate outgrowth above the respiratory orifice, kept in almost incessant motion by the animal. The Columellar Lobule, a somewhat triangular pallial process of the hinder margin, is also developed in some species and is especially noticeable in those forms in which the umbilicus is closed by a shelly deposit.

Fig. 397.—*Planorbis corneus* (L.), showing the exsertile Auriform Lobe (after Pelseneer). *r.l.* respiratory or auriform lobe.

In the Streptoneura of our fauna the instances of pallial outgrowths are few and insignificant. In *Vivipara*, the right mantle margin bears a number of slender but hollow processes of various sizes, which give rise to the spiral rows of minute hairs which encircle the young shell, and *Valvata* possesses a well developed pallial tentacle on the right side which has been thought to be the vestigial representative of the vanished, but primitively left ctenidium.

In the Pelecypoda similar processes evidently exist on the mantle of *Sphærium corneum*, whose shell when young bears numerous small and projecting hair-like processes.

The Enclosure of the shell within the mantle, owing to the extension and fusion of the pallial margins, is known to exist in exotic species belonging to each of the groups of mollusca represented in our fauna, yet it is only in the Euthyneures that we have species which enable us, though disconnectedly, to show some of the stages in this particular line of pallial specialization, which leads us from the typical *Helix*, with the mantle margins extending to or slightly overlapping the aperture of the shell, to *Arion*, with the shell covered in and practically lost by the overfolding of the mantle.

That *Arion* and other naked species are derived from forms with distinctly developed shells is shown not only by their retention of the vestiges of a shell, but by passing through a stage of development in which a distinct spiral shell, containing the intestinal sac, is present,

and the asymmetry of their internal organs and external orifices can only be satisfactorily explained as having been inherited from ancestors with spirally twisted intestinal sacs and shells.

In *Vitrina* we have the first distinct stage in this process of the degeneration of the shell by its enclosure within the pallial folds, which project anteriorly in the form of an incipient limacoid shield and laterally as a spatuliform lobe, both partially overspreading the external surface of the shell, which is evidently reduced in size as well as in substance, as the body of the animal is now only capable of being wholly contained within the shell during dry weather.

Physa fontinalis, though not a Stylommatophore, will serve to show a further advance in the development of the mantle lobes, as although they still have a very digitate character, especially on the left side, they have almost overspread the shell. The comparatively large size of the foot is due to the diminution in size of the shell.

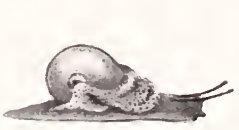


Fig. 398.

Fig. 399.

Fig. 400.

Illustrating the stages of the process leading to the degeneration and loss of the shell owing to its enclosure within the pallial lobes.

Fig. 398.—*Vitrina pellucida* (Müll.) × 1½, Horsforth, near Leeds, showing the first stages of pallial expansion. Fig. 399.—*Physa fontinalis* (L.) × 2, River Torne, Doncaster, illustrating a further advance of the process. Fig. 400.—*Amphipeplea glutinosa* (Müll.), Skidby Drain, Hull, collected by Mr. F. W. Fierke, in which the shell is almost entirely enveloped by the mantle.

Amphipeplea glutinosa, another Basommatophore, although able to entirely cover the shell by its extended pallial lobes, does not usually do so, a small rhomboidal dorsal space being generally left uncovered, enabling the maculate body of the animal to be seen through the transparent shell. The foot does not exhibit any disproportionate size in comparison with the size of the shell, owing to the degeneration the shell is undergoing having more especially affected its substance and not its magnitude. In all these cases it is instructive to observe the noticeable paucity in the number of whorls of the shell and the exceeding delicacy and tenuity of its substance, both characters induced by the overwrapping of the mantle lobes.

The genus *Arion* illustrates the disappearance of a definite shell, the anterior mantle or shield, as it is called, having assumed a very tough and leathery consistency, its margins completely overlapping and fusing together to form a sac enclosing the calcareous granulations which represent the vestigial shell.

When thus developed, the interior surface of the mantle having become permanently external, assumes special sculpture and markings in harmony with those of the body. In the *Limaces* it becomes more or less regularly concentrically furrowed, but in *Arion* these concentric wrinkles are not perceptible, the whole surface being somewhat uniformly granular, although during strong contraction an appearance of concentric striation is apparent at the anterior end. In *Amalia* the mantle, though simply rugose, displays a smooth, somewhat rhomboidal furrow, which is deepest on the right side; it is sub-angulate in front, rounded on the left side and distinctly angulate on the right, the point joining the anal furrow anterior to the respiratory orifice; its use may possibly be to drain some secretion into the mantle cleft.

FIG. 401.—*Arion hortensis* Fér., Horsforth, near Leeds, illustrating the complete infolding of the shell by the mantle and its consequent atrophy and loss.

In the Pelecypoda of our fauna we have no examples of such high pallial specialization as we find in the *Arionidæ* and *Limacidæ*, although such a form is actually known; the genus *Chlamydoconcha* having the mantle lobes so greatly developed that they have completely enclosed the shell, the valves of which have lost their connecting ligament and adductors and are now separately imbedded within the pallial lobes.

The REDUCTION IN SIZE of the mantle and shell may be in correlation with the detorsion of the visceral sac or from adaptation to special or peculiar habits of life, and we have a striking exemplification of this feature in the genus *Testacella*, a group of mollusks especially adapted to a subterranean existence, in which the visceral sac has become untwisted and the respiratory organs returned to the rear of the animal, the mantle being reduced to the smallest dimensions and placed at the extreme hinder end of the body, its shell forming a shield or protection at the rear while the creature is traversing the worm-burrows in search of the worms upon which it feeds.

FIG. 402.—*Testacella haliotidea* Drap., Oxford, collected by Prof. E. B. Poulton,

Illustrating the reduction of the mantle and shell resulting from the detorsion of the body and adaptation to a special mode of life, and incidentally showing the strongly marked lateral grooves.

With the atrophy or reduction of the shell and its predominant influence as a modifying factor lost, the foot, the body, and the mantle are free to develop such protective modifications in form, colour, texture or function as may be best adapted to compensate for its loss, such compensation may be by the development of a thicker and tougher integument, of a more abundant mucosity, or of colouring or markings harmonizing more closely with the usual surroundings of the animal ; in marine species, stinging cells, autotomy or voluntary amputations of portions of the body, and a great capacity for regeneration of injured parts may be instanced as some of the compensatory attributes that have been acquired.

The Visceral or Body Region.

The Body is usually more or less covered by the mantle, and consists in the testaceous species of the dorsally projecting, visceral sac and the connected cavity above the muscular foot. It varies in shape according to the genus and in the *Arionidæ* and *Limacidæ* the spirally coiled dorsal region, which characterizes the testaceous Gastropods,

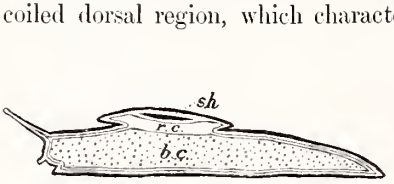


Fig. 403.

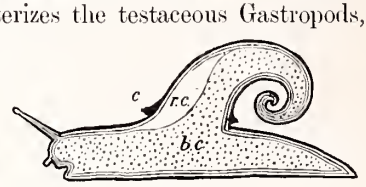


Fig. 404.

Diagrammatic sections showing the arrangement of the visceral sac, etc., in the coiled *Helicidæ* and the secondarily symmetrical *Limacidæ* (after Binney).

Fig. 403.—*Limax*. Fig. 404.—*Helix*. *b.c.* body or visceral cavity ; *c.* collar of mantle ; *r.c.* respiratory chamber ; *sh.* shell.

has become depressed and flattened out, so that all external trace of its former coiled condition is lost and a secondary external symmetry acquired; the mantle and shell being also reduced in size, the body region is consequently permanently exposed and its integument has therefore acquired a thicker and more coriaceous character.

The surface of the body, though generally thin, soft and flexible, is covered, in the terrestrial species, by more or less closely disposed and prominent rugosities, which vary in number and character according to the species, the interstices between them serving to distribute over the surface of the body the mucus poured forth by the glandular integument, but in addition to the local diffusion of the mucus thus secured, there are deep and longitudinally disposed grooves, which extend from the pallial region to the anterior part of the body, and give off during their course many subsidiary and ramifying branches.

The Dorsal Grooves form the principal longitudinal grooves or furrows; they are a pair of parallel and deeply marked channels, separated by a row of elongate tubercles, and extend from between the tentacles, along the centre of the back, and may be continued anteriorly upon the muzzle as the facial grooves.

FIG. 405. — *Succinea putris* (L.) × 3, Christchurch, Hants., showing the dorsal grooves.

The Lateral Grooves are distinctly developed only in the testaceous forms, the right lateral groove arising near the pneumostome and reaching to the base of the tentacle near the genital opening, the left groove when present having a similar course; and the tubercles or rugosities of the body being usually noticeably larger and more oblong above the grooves than beneath, this difference in character being sometimes very sharply marked. These grooves, though now only serving to assist in the dissemination of the fluid mucus over the body, probably indicate the position of the ciliated conduit, which formerly conveyed the seminal fluid from the genital glands to the male organ; they are especially developed in *Testacella*, arising together beneath the anterior margin of the mantle, and traversing the sides of the body, giving off during their course a number of anteriorly directed furrows, whose ramifications are gradually obliterated in the general roughness of the integument.

FIG. 406.—*Hyalinia helvetica* Blum × 2, Horsforth, near Leeds, showing the lateral grooves.

In the Pelecypoda the usually oval body, being entirely enclosed by the mantle lobes, is soft, smooth and somewhat strongly ciliated, but the viscera have also become deeply sunk within the foot.

In the Anisopleurous Gastropods, the dorsally protruding body has been subjected to a very remarkable and combined antero-ventral and lateral twisting or torsion, which renders it more compact and brings together the opposite ends of the alimentary canal. Such torsion is, however, not confined to Gastropods, or even to mollusca, as analogous processes have been observed to take place in Crustacea, Bryozoa, Echinoderms and other forms of life.

The ontogenetic history shows this twisting in the Gastropods to occur before anything else which alters the primitive form, as the

animal is strictly symmetrical up to the Trochosphere stage, the pallial cavity being then in the rear, as in the hypothetical primitive mollusk, but is brought to the front above the neck by the cessation on the right side of the embryo of the growth, which is uninterruptedly continued on the left. This torsion, effected during development in the Streptoneures, is also manifest in the Euthyneures at the commencement of embryonic life, but becomes indefinite and in great part lost at a later stage by a movement or twisting in the opposite direction.

The Antero-ventral torsion to which the primitive exogastric inclination of the body is due, probably arose on account of the increasing size of the foot separating more and more widely the anterior and posterior openings of the alimentary canal. The lateral twist of the body, with which the antero-ventral torsion is practically combined, is owing to the continually increasing protrusion of the hernia-like visceral dome and the development upon it of a long, heavy shell, giving protection to and a means of concealment for the entire animal, which was gradually becoming more actively reptant.

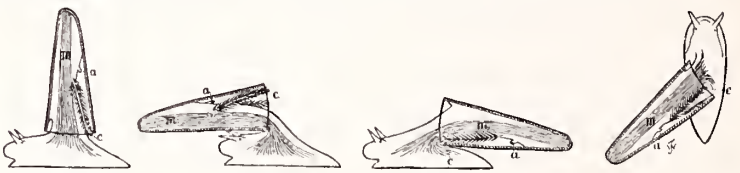


Fig. 407. Fig. 408. Fig. 409. Fig. 410.

Diagrams illustrating the various positions which it is possible for the hypothetical, unwieldy elongated shell to assume (after Lang). *m.* columellar muscle ; *c.* ctenidia or gills ; *a.* anus.

Fig. 407 shows the shell in its hypothetical primitively upright position.

Fig. 408 shows the shell forwardly inclined, the most unfavourable position for locomotion, but the most favourable imaginable for the exercise of the functions of the posterior pallial organs.

Fig. 409 shows the shell inclined to the rear, the most favourable position for locomotion, but the most unfavourable for the exercise of the functions of the organs confined within the compressed mantle cavity.

Fig. 410 shows the shell inclined to the left side, the position it would most probably assume as combining least interference with locomotion and with the exercise of the functions of the posteriorly placed pallial organs.

As seen by the illustrative figures, when the shell became so unwieldy from its increasingly elongate form and necessarily unstable equilibrium that it could no longer be conveniently carried in an upright position, it would probably gradually lean over to one side, which, all things considered, would be the most favourable position it could occupy, but during locomotion, it would naturally tend to become more posteriorly directed.

In this position the compression due to the recumbent shell would bear heavily upon the organs placed at the left side of the body, if the shell leaned over to that side, and the compressed organs would

gradually become displaced and move towards the right side of the body, which would be favourably influenced for their reception by the strain of the shell upon the opposite side, and the shell would become more and more posteriorly placed according as the organs beneath moved round towards the right, to attain the most favourable position for the free exercise of their functions, which would be the side of the body opposite to that upon which the shell was recumbent, until owing to the constant tendency of the shell to take up a position in the rear as that most favourable to locomotion, and the equally constant and correlated movement of the organs to attain a position opposite to it as offering least interference with their functions, the pallial organs eventually occupy the anterior part of the body opposite the shell, which has at length definitely assumed the posterior position most favourable to locomotion, and also to the free action of the now anteriorly placed respiratory and excretory organs.

FIG. 411. — Diagram illustrating the graduation of the compression or strain to which the visceral dome is subject if the shell he inclined to the left (after Lang). The thickest lines indicate the point of greatest compression and the thinnest lines the point of least compression. The arrows indicate the direction in which the twisting takes place, owing to the position of the shell on the left side.

But when the shell became long and unwieldy and tended to fall over to the side of the animal, the body and shell could no longer retain their simple conical shape, as owing to the lateral inclination of the shell the base of the visceral dome would be uncovered at the right side if the inclination of the shell was to the left, and the growth necessary to protect the part thus uncovered would necessitate a quicker increase there, which would consequently be the point of maximum growth and become convex, while the opposite or underside would be the point of minimum growth and become concave. If the shell retained the same position during growth a discoid shell would be produced, but if the growing shell on account of its shape, increasing weight, or other cause becomes altered in position towards the right the point of maximum growth would be changed and the spirally coiled dextral shell and visceral sac would result, which the now asymmetrical pallial cavity has assisted to perpetuate.

The long continuance of the unfavourable conditions to which the primitively left organs of the pallial complex were subjected by the compression due to the heavy external shell, eventually brought about their more or less complete degeneration and loss, thus leaving vacant

the space at the anterior right side of the pallial cavity which the atrophied organs would normally have occupied; the organs of the left side of the cavity have, however, moved backwards towards the right and filled the vacant space; by this unwinding movement or practical partial detorsion the anus, which was placed near the median line above the neck, eventually came to occupy a position at the extreme right of the mantle cavity.

In the Streptoneures this torsion of the body is greater than in the other groups, but the asymmetry of the internal organs is not always so complete as in the less distinctly twisted Euthyneures, some genera still retaining the primitively paired gills, nephridia, and other organs, but the pallial opening is placed at the front, over the neck of the animal, and the pleuro-abdominal commissures are crossed, both circumstances owing to the twisting undergone by the body.

In the Euthyneures, although the twisting of the body is less, as shown by the lateral opening of the pallial cavity and the relative positions of the pallial organs, yet the asymmetry of the internal organs is greater, as all traces of the originally left half of the primitively paired organs have disappeared and renders reasonable the supposition of Prof. Pelseneer that the Euthyneures are to be regarded as derived from and as in a more advanced stage of specialization than the Streptoneures, which are our most primitive forms and that the less amount of body twist and greater internal asymmetry they exhibit is owing to a process of partial detorsion which the Euthyneures have probably undergone; all those animals whose visceral dome has undergone complete detorsion, as shown by the return of the respiratory and other organs to their primitive position at the rear of the animal, are liable to the disappearance or partial atrophy of the mantle and shell, as strikingly shown in the Opisthobranchs and in the terrestrial genus *Testacella*, which is distinctly opisthopneumonic, the respiratory organs being now posterior to the heart.

Although our Pelecypods show little sign of having undergone any noticeable torsion of the body, except such coiling as the Prosogyrate umbones indicate, yet the group is not exempt from it, as the animals of the genus *Tridacna* clearly show that their body in its relation to the shell has been subjected to an anterior rotation or twist of nearly 180°, which has brought the posterior adductor muscle to near the ventral margin of the shell and the mouth or oral aperture close to the umbones.

The Internal Organization.

The internal organization of the mollusca is characterized by a certain degree of uniformity due to the common origin of the phylum, but this general ancestral likeness has been partially obliterated by the development of adaptive characters, more especially correlative with the special habits of the animals.

NERVOUS SYSTEM.

The nervous system, upon which sensation and muscular motion depend, resembles in some respects that of Vermes; it is of paramount importance in the animal organization, while being the last to be influenced by the morphological modifications undergone by the animal, its peculiarities acquire very great phylogenetic significance, and have been used by Schimkewitsch as the basis for the classification of all Bilateralia, the mollusca being termed Tetraneura, and characterized by the possession of cephalic ganglia, with paired ventral and lateral nervous cords. It is also more generally used in a restricted way to separate two great groups of Gastropods, according as the pleuro-abdominal commissures are straight or still twisted by the torsion which the body of the animal has undergone.

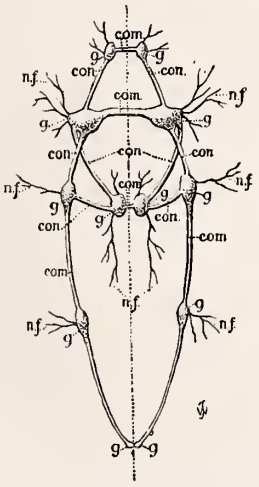


Fig. 412.—Diagram of the nervous system of a mollusk, showing the bilateral arrangement of its constituent parts and their relation to the median line of the body.

g. ganglia, or paired aggregations of nervous tissue; *con*. connectives, the longitudinal nerve cords joining dissimilar ganglia and never crossing the median line of the body; *com*. commissures or transverse nerve cords, connecting the moities of the same ganglionic centre and therefore always crossing the median line of the body; *n.f*. nerve fibrils.

The nervous system consists essentially of nucleated ganglion cells and nerve fibres, forming Ganglia, Connectives, Commissures, and Nerve Fibrils, which are invested by the Neurilemma, a somewhat fibrous and more or less deeply pigmented sheath of connective tissue. Although primitively characterized by the absence of any local concentration of its various parts, which were probably constituted by ganglionic nerve cords, such as still represent the pedal ganglia of *Vivipara*, yet usually the nervous tissue has now

become decidedly concentrated and forms enlargements or ganglia in various parts of the body, which are connected together by nervous cords and give rise to innumerable delicate nerve fibrils, whose ramifications extend to all parts of the animal.

The Ganglia are the most important part of the nervous system, and are constituted by concentrated masses of whitish, or somewhat pigmented, nerve tissue, which arise during embryonal development by the thickening and subsequent invagination of the epiblast or

Fig. 413. Fig. 414. Fig. 415.

Fig. 413.—Unipolar and Multipolar ganglion cells from visceral ganglion of *Anodonta anatina* (L.), × 500 (after Rawitz). Fig. 414 Bipolar and Fig. 415 Multipolar ganglion cells from the osphradium of *Limnæa stagnalis* (L.), highly magnified (after Simroth).

integument. They are composed of ganglion cells of variable size, each of which may be furnished with some minutely delicate processes called Dendrites, and one or more strong fibrillar prolongations, the cells being known as Unipolar, Bipolar or Multipolar, in accordance with the number of these important nerve fibres emanating from them;

Fig. 416. Fig. 417.

Fig. 416.—Axis cylinder of the visceral ganglion cells of *Unio pictorum* (L.) × 500 (after Rawitz).
Fig. 417.—Axis cylinder of the cerebral ganglion cells of *Anodonta anatina* (L.) × 500 (after Rawitz).

these various prolongations are furnished with a central core or axis cylinder, and serve to connect the constituent cells of the ganglia with each other and with other parts of the nervous system.

The ganglion cells, however, differ in their arrangement from that obtaining in the Vertebrates, as they are disposed radially around the central portion or nucleus, which is constituted by the aggregation of their fibrillar prolongations, and also gives origin to the more homogeneous nerve fibrils. Small spherical cells exist only in the more anterior lobes of the cerebral ganglia or its connections and are assumed to be the seat of the more specialized sensory faculties. During rest the ganglion cells store up nervous energy and also chromatophilous substances which become used up during their

activity. Exercise or the transmission of nervous stimuli is always accompanied by enlargement of the nerve cells and their nuclei, and exhaustion is shown by their shrivelling and the presence of diffuse chromatin therein.

Ganglia may be of a primary, secondary, or accessory character. The primary ganglia are the large compact and paired nerve masses, which have their moities placed at opposite sides of the body, but connected together by commissures, which always cross the median longitudinal line; they comprise the cerebral or supra-œsophageal ganglia and the ganglia directly connected therewith by paired connectives; the secondary or commissural ganglia are the lesser nerve masses which are more or less closely associated together to form the compound visceral ganglia; and the accessory nerve masses are the small additional ganglia developed on the courses of the various nerves to subserve some special function.

The Connectives are important nerve trunks richly furnished with ganglion cells along their whole course; they are always longitudinally directed and do not cross the median line, but connect together the ganglia at the same side of the body. The three connectives which primitively originate from the right cerebral ganglion are the cerebro-pedal, which connects the right cerebral and the right pedal ganglia; the cerebro-pleural, which joins the right cerebral and the right pleural ganglia; and the cerebro-buccal, which unites the right cerebral with the right buccal or stomato-gastric ganglion, when the latter are recognizably present; the left cerebral ganglion is similarly joined to the left moities of the other ganglia, and in addition the right and left pedal ganglia are also united with the right and left pleural ganglia by the pleuro-pedal connectives.

Fig. 418.—Section through cerebro-pleuro-pedal connective of *Unio pictorum* (L.), showing the ganglion cells interspersed amongst the nerve substance, × 175 (after Rawitz).

The Commissures are transverse nerve cords, usually with few ganglion cells, which cross the median line of the body more or less directly and connect together the moities of the same ganglionic centre placed at opposite sides of the median line; thus the cerebral commissure joins the right and left moities of the cerebral ganglia above the œsophagus, while the remaining ganglia, the pedal, the visceral, and the buccal or stomato-gastric, are similarly connected beneath it.

The Nerve Fibrils are the delicate whitish nerve threads, composed nearly exclusively of parallel longitudinal filaments arising directly from the ganglia or from the various nerve cords, and whose minute ramifications extend to every part of the body; they act as conductors or conveyors of nerve force or stimuli, to and from the various ganglia and the different organs without affecting the intervening tissues through which they necessarily pass; they may be divided, according to their function, into Afferent or Sensory and Efferent or Motor nerves.

The Afferent nerves terminate on the surface of the body or within the sensory organs, in the form of suitably modified neuro-epithelial cells, and convey tactile or more distinctly specialized acts of perception to the cerebral or other ganglia, and also connect together the

Fig. 419.—Afferent nerve fibre, connecting the integumental neuro-epithelial cell with the sensory ganglion cell, within which is the nuclear network and the nucleolus, × 600 (after Bernard).

sensory cells therein. At the surface of the body they form slender and fusiform, or externally expanded cells, sometimes bearing tufts of sensory hairs, but the ends may also become divided and distributed within the integument.

The Efferent nerves unite together the motor cells of the ganglia, and convey nervous impulses or impressions from the ganglia to the various organs of the body. The efferent nerves may be of a Motor, Sympathetic or Inhibitory character. The Motor nerves are those which terminate within and excite contractions of the muscles of the body, or if distributed amongst the glands, excite a more abundant

Fig. 420.—Efferent nerve fibre, with the motor ganglion cell, from which it arises, and showing its connection to a muscle cell, × 600 (modified after Boas).

flow of their secretions; the Sympathetic nerves regulate the involuntary and more or less rhythmical motions of the internal organs, while the Inhibitory nerves, which chiefly or solely arise from the cerebral ganglia, affect the action of all other nerve centres, moderating or annulling their influence. The afferent and efferent nerves traverse the organs together, but are quite distinct and equally cease to act when their connection with the centre is interrupted or destroyed.

In the Mollusca there are generally four chief nerve masses or ganglia, which may be broadly classified as Supra-œsophageal and Sub-œsophageal, according to their position above or beneath the alimentary canal. The supra-œsophageal nerve mass is composed solely of the Cerebral or Sensory ganglia, while the compound sub-œsophageal group is formed by the Pedal or Motor ganglia, and the Visceral and the Buccal or Stomato-gastric centres, which to a certain extent are comparable to a sympathetic system. The cerebral and pedal ganglia are essentially nerve centres for the ectodermic organs, the buccal ganglia for those of the endoderm and the combined visceral centre for those of mesodermic origin. All these centres are each more or less distinctly paired in correlation with the bilateral arrangement of many of the organs of the body, but they are all

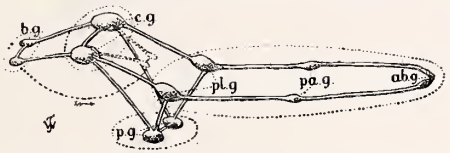


FIG. 421.—Diagrammatic obliquely dorsal view of the nervous system of a Gastropod, showing the four nerve centres and their commissures enclosed separately within dotted lines.

b.g. paired buccal ganglia (the curved line and arrow indicate the change in position they undergo in some species by the retraction of the buccal bulb); *c.g.* paired cerebral ganglia; *p.g.* paired pedal ganglia; the compound visceral centre is also enclosed by a dotted line and is formed by the *pl.g.* pleural ganglia, *pa.g.* pallial ganglia, and *ab.g.* abdominal ganglion.

liable to vary in size and importance and in the amount or mode of fusion with each other or with neighbouring ganglia in accordance with the specialization the animal or its organs have undergone.

The GASTROPODA, in their nervous system, exhibit throughout our British species the four normal paired nerve centres, which form three more or less confluent nerve loops encircling the alimentary canal, all of which arise from the supra-œsophageal ganglia, and, according as they do or do not exhibit a twist or crossing of the posterior nerve cords, have been distinguished as Streptoneura and Euthyneura respectively.

The STREPTONEURA or Chiastoneura constitute a group practically co-extensive with the older groups Prosobranchiata and Operculata, and is composed of the most primitive and archaic of our species, the nervous system being still characterized by the innervation of the male organ of reproduction from the pedal ganglia, by the widely separated visceral centres, and more especially by the remarkable crossing of the pleuro-abdominal commissures arising from the semi-rotation of the visceral sac.

In the EUTHYNEURA the male organ is innervated fromt he cerebral and not from the pedal ganglia, and the pleuro-abdominal commissures do not exhibit the crossing that so markedly characterizes the Streptoneures, but Prof. Pelseneer has demonstrated the probability of the former existence of a similar torsion which is shown not only by the retention of a partial streptoneury by some of the more archaic pulmonate genera, but by the right pallial ganglion still occupying a more elevated position than the left, perhaps due to its previous supra-intestinal position.

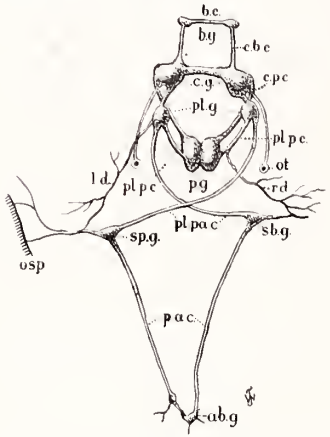


FIG. 422.

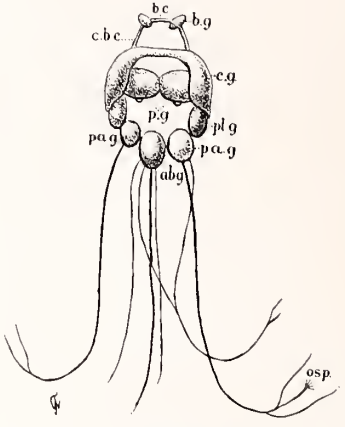


FIG. 423.

FIG. 422.—Diagram of the nervous system of a Streptoneure, *Cyclostoma elegans* (Müll.), showing the characteristic crossing of the pleuro-abdominal commissures, and the consequent transference to the left side of the body of the morphologically right osphradium (after Lacaze-Duthiers).

FIG. 423.—Diagram of the nervous system of an Euthyneure, *Limnæa peregra* (Müll.), showing the concentration of the visceral ganglia and the dextral position of the morphologically right osphradium (modified after Spengel).

ab.g. abdominal ganglion; *b.c.* buccal commissure; *b.g.* buccal ganglia; *c.b.c.* cerebro-buccal connectives; *c.g.* cerebral ganglia; *c.p.c.* cerebro-pedal connectives; *l.d.* left dialyneurous nerve; *ot.* otocyst; *osp.* osphradium; *p.g.* pedal ganglia; *pa.g.* pallial ganglia; *pl.g.* pleural ganglia; *pl.p.c.* pleuro-pedal connectives; *pl.pa.c.* pleuro-pallial commissures; *p.a.c.* pleuro-abdominal commissures; *r.d.* right dialyneurous nerve; *sb.g.* subintestinal ganglion; *sp.g.* supra-intestinal ganglion.

In the Stylommatophora the greatest amount of specialization is exhibited, the various ganglia having become more or less closely aggregated around the pharynx, behind the buccal bulb, by the shortening of the connectives and commissures, the buccal bulb being capable of withdrawal or protrusion through the cerebro-visceral nerve loop, as in *Helix aspersa* and other species, but in some genera, as *Succinea*, the cerebro-pleural connectives have by specialization become so short and the cerebro-visceral opening so contracted thereby that the buccal bulb cannot be withdrawn through the nerve-ring, and is therefore practically immoveable.

The Basommatophora do not exhibit so marked a concentration of the ganglia as is shown by the Stylommatophora, but *Planorbis* displays the same constriction of the cerebro-visceral nerve ring

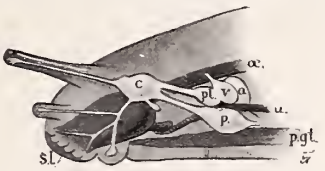


Fig. 424.—Semi-schematic view of the prosoma of *Limax*, showing the arrangement of the ganglia, nerves and other organs and their relation to the protrusible and retractile buccal bulb, × 3 (after Pelseneer).

a. abdominal ganglion; *c.* cerebral ganglia, with the infero-posterior buccal ganglia and also showing nerve prolongations to the eyes, rhinophores, labial lobes, Semper's lobes, etc.; *æ.* œsophagus; *p.* pedal ganglia; *p.gl.* pedal gland; *pl.* pleural ganglia; *S.l.* Semper's lobes; *u.* anterior aorta: *v.* visceral or pallial ganglia.

Fig. 425. — The buccal bulb of *Succinea putris* (L.), showing the close constriction of the cerebro-visceral nerve ring around the œsophagus, cephalic retractors and salivary ducts, owing to the shortening of the cerebro-pleural connectives, which totally prevents the retraction of the buccal bulb through the nerve ring, × 8.

around the œsophagus as exists in *Succinea*, which equally prevents the withdrawal of the buccal bulb.

In the Pelecypoda the nervous system is quite symmetrical and apparently simpler in character than in the Gastropods, but this chiefly arises from the fusion and combination of ganglia which are

Diagrammatic dorsally oblique views of the nervous system, to show the mode by which the apparently simpler nervous organization of the Pelecypoda has arisen from the more complicated arrangement of their assumed ancestor.

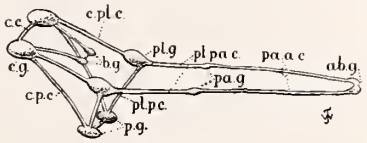


Fig. 426.

Fig. 426. — Nervous system of a primitive mollusk, showing the posteriorly directed buccal ganglia, the distinct pleural and pallial centres, and the paired abdominal ganglia.

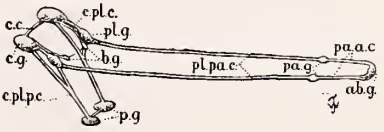


Fig. 427.

Fig. 427.—An intermediate stage, showing the approximation of the pallial and abdominal and of the cerebral and pleural ganglia, which eventually fuse and form the visceral or parieto-splanchnic and the cerebro-pleural ganglia respectively of the Pelecypoda, the cerebro-pedal and the pleuro-pedal connectives also combining in a part of their course owing to the increasing approximation of the pleural to the cerebral ganglia; the buccal ganglia also tend to combine with the cerebro-abdominal nerve cords.

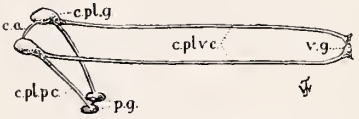


Fig. 428.

Fig. 428.—Nervous system of a Pelecypod, showing the completion of the fusion of the cerebral and pleural ganglia, and of the pallial and abdominal ganglia to form the cerebro-pleural and visceral ganglia respectively. The buccal ganglia and connectives are completely fused with the commissures from the cerebro-pleural ganglia, and the cerebro-pedal and cerebro-pleural connectives have also become intimately joined together.

ab.g. abdominal ganglia; *b.g.* buccal ganglia; *c.c.* cerebral commissure; *c.g.* cerebral ganglia; *c.p.c.* cerebro-pedal connective; *c.pl.p.c.* cerebro-pleuro-pedal connective; *c.pl.v.c.* cerebro-pleuro-visceral commissures; *c.pl.c.* cerebro-pleural connective; *c.pl.g.* cerebro-pleural ganglia; *pa.a.c.* pallio-abdominal commissures; *pa.g.* pallial ganglia; *p.g.* pedal ganglia; *pl.g.* pleural ganglia; *pl.pa.c.* pleuro-pallial commissures; *pl.p.c.* pleuro-pedal connective; *v.g.* visceral ganglia.

often distinctly separated in Gastropods. Usually there are only three distinct but widely separated nervous masses, known as the

cerebro-pleural, the pedal and the visceral or parieto-splanchnic centres, which are joined together by connectives and commissures forming two nerve loops encircling the alimentary canal, the long and important cerebro-pleuro-visceral commissures, which extend almost the whole length of the body, containing many ganglion cells.

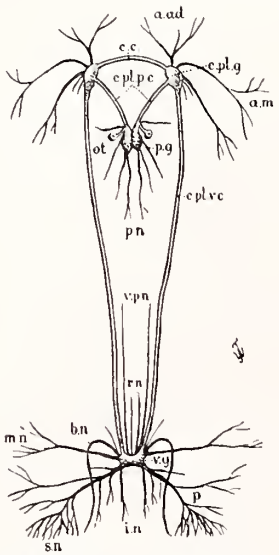


Fig. 129.–Diagram of the nervous system of a Pelecypod, *Anodonta cygnea* (L.).

a.ad. anterior adductor nerves; *a.m.* anterior mantle nerves; *b.n.* branchial nerves; *c.c.* cerebral commissure; *c.pl.g.* cerebro-pleural ganglia; *c.pl.p.c.* cerebro-pleuro-pedal connectives; *c.pl.v.c.* cerebro-pleuro-visceral commissure; *i.n.* rectal and cardiac nerves; *m.n.* median mantle nerves; *ot.* otocyst; *p.* posterior mantle nerves; *p.n.* pedal nerves; *r.n.* renal nerves; *s.n.* nerves to siphonal tentacles; *v.g.* visceral ganglion; *v.p.n.* nerves along kidney to hinder part of foot.

The efferent nerves, which give rise to the contraction of the adductor muscles, always arise from the ganglia in their immediate proximity, but the inhibitory nerve fibres, which produce their relaxation and allow the shell to gape owing to the elasticity of the ligament, are stated to arise exclusively from the cerebral ganglia.

The buccal or stomato-gastric and the pleural ganglia and the pleuro-pedal connective, which were formerly considered as peculiarly characteristic of the Gastropoda, are also really present in Pelecypods, but are usually so intimately fused with the neighbouring parts of the nervous system that their combination can only be satisfactorily demonstrated by the microscopical examinations of suitable sections.

The Cerebral or Sensory ganglia, sometimes also termed the buccal, supra-œsophageal or post-œsophageal ganglia, originate as a paired epiblastic thickening within the velar area and are sometimes fused together, but when separate the constituent parts are joined by commissures above the œsophagus, by the side of which these ganglia are placed. In addition to innervating the head and its sensory organs, they give off branches to the anterior body wall and to the otocysts, and are the chief point of convergence of the afferent nerves, but vary in development in correlation with the functional importance of the organs innervated, and are joined by connectives with the sub-œsophageal centres forming nerve loops which surround the alimentary canal.

In the most primitive Streptoneures the cerebral ganglia are joined in front of the buccal mass, but behind it in the more specialized forms; in *Vivipara* and *Neritina* there is an additional but sub-œsophageal cerebral commissure, distinguished as the labial commissure, which passes beneath the œsophagus, and forms a fourth nerve collar around the alimentary canal.

In the Stylommatophora the cerebral ganglia are closely approximated dorsally, and distinct regions, from which special groups of nerves originate, are distinguishable therein, which have therefore been differentiated as the Protocerebron, Mesocerebron, and Metacerebron. In the anterior protocerebral region, as well as in the terminal ganglia of the upper and lower tentacles and labial lobes, small spherical sensory ganglion cells of uniform size are congregated, and in *Helix pomatia* especially the ganglion cells of the cerebral ganglia are more differentiated in size and polarity than those of the Basommatophora.

Fig. 430. — Cerebral ganglion cells, with their nerve prolongations, from *Anodonta anatina* (L.), × 500 (after Rawitz).

Electrical or mechanical stimulation of the cerebral ganglia of *Helix* produces little or no perceptible effect, and the animal can survive their removal for four or five weeks, although remaining perfectly motionless.

In the Pelecypoda the supra-œsophageal or cerebro-pleural ganglia are generally small in correlation with the diminished importance of the cephalic region. They are placed near the pedal protractor and innervate the anterior adductor, the labial lobes, and the oral region generally, besides giving off the anterior pallial nerves, which ramify within the pallial margin and unite with the posterior pallial nerves arising from the visceral ganglia. They also furnish the nerves to the otocysts and, according to Pelseneer, to the osphradia also, and are composed of the cerebral ganglia united with the pleural ganglia of the visceral centre. This combination of the ganglia is clearly shown in the archaic genus *Nucula*, in which the pleural ganglia, though in close proximity, have not yet fused with the cere-

bral centre, and consequently the pleuro-pedal connectives are still distinct from the cerebro-pedal connectives, with which, in most species, they are intimately fused to form the compound cerebro-pleuro-pedal connective.

The Pedal ganglia, also called the antero-inferior or subœsophageal ganglia, are placed beneath the œsophagus and within or near the foot and are more especially motor; they are earlier in development and more constant in their character than the visceral centres, and innervate the foot and its dependencies, being correlated in size with its development; they are joined with the cerebral and visceral ganglia by paired connectives and are usually in intimate association with the otocysts.

Fig. 431.—Pedal ganglion cells, with their nerve prolongations, from *Unio pictorum* (L.), × 500 (after Rawitz).

In many Streptoneures the pedal ganglia still retain the archaic character of long ganglionic nerve cords, traversing the foot longitudinally and united at intervals by numerous slender commissural fibrils, in addition to the chief pedal commissure at the anterior end of the foot, near the junction of the cerebral and visceral connectives. The regular repetition of these slender commissures recalls the ladder-like arrangement of the pedal nerves in the Isopleura. The male organ of reproduction is of pedal nature and usually innervated by the pedal ganglia.

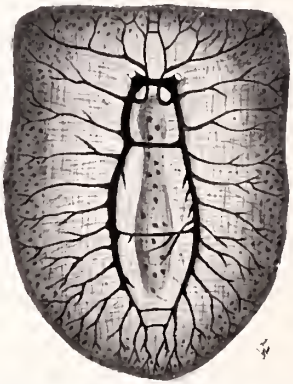


Fig. 432.—Sole of *Vivipara vivipara* (L.) to show the pedal nerve cords, which represent the pedal ganglia and also showing the central pedal blood sinus, × 3 (after Simroth).

In the Euthyneura the pedal ganglia have generally become intimately fused and approximated to the ventral side of the œsophagus, and usually bear the otocysts adherent to or actually imbedded in their under surface.

Electrical or mechanical stimulation of the subœsophageal ganglia of *Helix* causes vigorous muscular agitation, but the animal only survives their removal about twenty-four hours.

Some Opisthobranchs possess in addition to the usual commissural connection between the pedal ganglia, a second, or as it is termed, a parapedal commissure.

In the Pelecypoda the pedal ganglia are usually placed at the root of the foot near the junction of the visceral and muscular parts, and usually partially or closely fused together, with the otocysts in close proximity, although the otocystic nerves arise from the cerebral centre.

The Buccal or Stomato-gastric ganglia are usually placed near the outlet of the salivary ducts, and vary greatly in their position in relation to the cerebral ganglia, according to the amount of protrusion of the buccal bulb; they are connected together beneath the origin of the œsophagus, and, unlike other centres, are connected solely with the cerebral ganglia, and have only indirect communication with the pedal or visceral ganglia ; they innervate the stomach, œsophagus, salivary glands, anterior aorta, the pharyngeal muscles, etc., and are to some extent sympathetic in function.

In the Streptoneura they were primitively permanently posterior to the cerebral ganglia, which were fixed in advance of the buccal bulb, but in many of the Euthyneures and more highly developed Streptoneures, the buccal bulb is capable of protrusion beyond or retraction behind the cerebro-visceral nerve ring ; and as the buccal ganglia are fixed beneath the origin of the œsophagus, they participate in its movements and may therefore be in front of or behind the cerebral ganglia according to the state of protrusion or retraction of the buccal mass.

In the Pelecypoda the buccal or stomato-gastric ganglia, which in the primitive mollusk innervated the anterior portion of the alimentary canal, are not apparent, but in correlation with the diminished importance of the head region, have degenerated and probably fused with the cerebro-pleuro-visceral commissures, which now supply the nerves to the early course of the alimentary tract.

The Visceral ganglia, variously named the parieto-splanchnic, viscero-pleural, postero-superior, median or inferior, may be regarded as the characteristic nerve centre of the mollusca, and chiefly innervate the mesodermic organs; they are usually unsymmetrical

and composed of several distinct, secondary ganglionic enlargements, known as the pleural, the pallial or visceral, and the abdominal ganglia, which are developed upon the course of the commissure, which connects together the moities of the pleural ganglia and would appear to correspond with the pleuro-visceral cords of the Isopleura, they innervate the circulatory, the reproductive and the excretory organs.

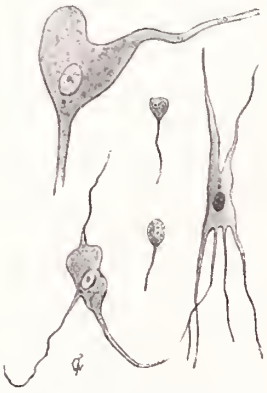


FIG. 433.—Visceral ganglion cells with their nerve prolongations, from *Unio pictorum* (L.), × 500 (after Rawitz).

The Pleural constituents of the visceral centre are the most anteriorly placed, and it is naturally with them that the cerebral and pedal connectives are joined. They are exceedingly unstable in position, not only in reference to their degree of approximation with the associated ganglia of their special group, but to other centres, as they may fuse into one mass with their own centre, or become intimately fused with the cerebral or with the pedal ganglia, and widely separated from their true position and associations; they chiefly innervate the mantle, the columellar muscle, and the body wall behind the head.

The Pallial, parietal, intestinal or visceral ganglia, as they are variously termed, have been supposed to represent, in a concentrated form, the many nerves supplying the gill leaflets in the Isopleura; they innervate the respiratory organs, the osphradia and the mantle generally, and are developed upon the pleuro-abdominal commissures, and when distinct from the abdominal centre divide them each into an anterior Pleuro-pallial commissure, uniting the pleural and pallial ganglia, and a posterior Pallio-abdominal commissure connecting the pallial with the Abdominal ganglion, the latter ganglion terminates the nerve loop and more especially innervates the genital gland and viscera, and although now usually apparently single, has probably arisen by fusion from a primitively paired condition.

In the Streptoneura the visceral ganglia are often much scattered and a considerable distance apart, and owing to the rotation of the visceral dome, described at page 206 *et seq.*, the organs originally occupying the right side of the mantle cavity at the rear of the animal have become transferred to the left side above the neck, and the

originally left posterior organs become placed on the right side of the now anterior mantle cavity, and as the pallial ganglia have been involved in this movement, the originally right pallial ganglion has passed to the left side of the body above the intestine, and has therefore been distinguished as the Supra-intestinal ganglion, and innervates the primitively right ctenidium and osphradium, which the torsion of the body has also transferred to the left side of the anterior pallial cavity, while the primitively left pallial ganglion has passed beneath the

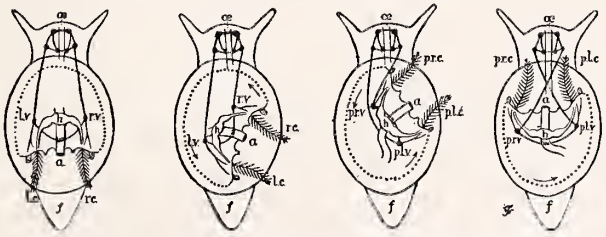


FIG. 434. FIG. 435. FIG. 436. FIG. 437.

Diagrams illustrating the process by which the crossing of the visceral nerves or Streptoneury is accomplished (after Lang). Fig. 434 shows the primitive untwisted condition of the nerves. Fig. 435 and Fig. 436 show the process partially accomplished, and Fig. 437 shows the crossing of the commissures completed, the semi-rotation of the visceral sac being accomplished. The arrows indicate the direction of the movement.

a. anus; *f.* foot; *h.* heart; *l.c.* left ctenidium, with osphradium at base; *l.v.* left visceral or pallial ganglion; *œ.* œsophagus; *p.l.c.* primitively left ctenidium and osphradium, now however placed on the actual right of the body owing to the rotation of the visceral sac; *p.l.v.* primitively left, but now the actually right visceral or pallial ganglion; *p.r.c.* primitively right, but now the actually left ctenidium and osphradium; *p.r.v.* primitively right, but now actually left visceral or pallial ganglion; *r.c.* right ctenidium and osphradium; *r.v.* right visceral or pallial ganglion.

intestine to the right side of the body and is now known as the Sub-intestinal ganglion; the commissures connecting these ganglia to the pleural and abdominal ganglia, which were straight and untwisted in the hypothetical primitive mollusk, are by this movement crossed and form a figure of 8, this feature constituting Streptoneury.

In the Euthyneura the aggregation of the various constituents of the visceral ganglia is carried out to the greatest extent, the whole of the ganglia having usually become more or less concentrated and fused together around the pharynx, owing to which and to the partial detorsion the visceral sac has undergone, the pleuro-abdominal commissures are not crossed and the osphradium, when retained, is placed at the side of the body to which it morphologically belongs, while the increased importance of the cephalic region, and the reduction and displacement of the mantle posteriorly has resulted in the innervation of the mantle devolving upon the pallial ganglia.

In the Pelecypoda the visceral or parieto-splanchnic ganglia are widely distant from the cerebro-pleural centre, and as the pleural

constituents of this centre have by specialization become quite separated and fused with the cerebral ganglia, are probably formed by the fusion of the pallial and abdominal centres of the primitive mollusk, the moities of this centre being however still separate in the primitive genus *Nucula*. The visceral ganglia are usually in contact with and ventral to the posterior adductor muscle and innervate the gills, the posterior adductor, and the viscera generally. They also give origin to the posterior pallial plexus, which innervates the respiratory orifices and the mantle margins and fuses midway therein with the pallial nerve from the cerebro-pleural ganglia.

The term Orthoneuroid was formerly applied to the nervous system of *Neritina* and *Helicina*, the supra-intestinal commissure and ganglion being stated to be deficient in those groups, and the crossing of the pleuro-abdominal commissures, characteristic of the Streptoneura, being consequently denied to exist. This belief is, however, erroneous, as no truly orthoneuroid mollusks are known.

Dialyneury exists only in the Streptoneura and consists in the establishment of a direct nerve connection between the constituent ganglia of the visceral centre, morphologically belonging to opposite sides of the body; this connection arising on the left side by the

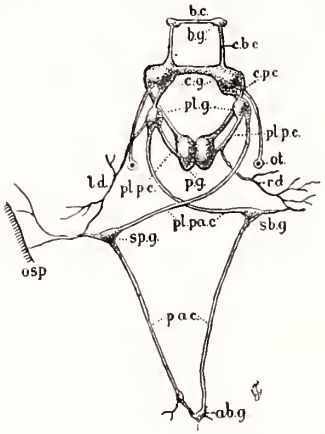


Fig. 438. — Nervous system of *Cyclostoma elegans* (Müll.), illustrating Dialyneury (after Lacaze-Duthiers).

l.d. nerve from the left pleural ganglion fused with the pallial branchial nerve, arising from the supra-intestinal ganglion and forming left Dialyneury; *r.d.* nerve from the right pleuro-pedal connective anastomosing with the pallial nerve from the subintestinal ganglion and constituting right Dialyneury.

ab.g. abdominal ganglion; *b.c.* buccal commissure; *b.g.* buccal ganglia; *c.b.c.* cerebro-buccal connective; *c.g.* cerebral ganglia; *c.p.c.* cerebro-pedal connective; *ot.* otocyst; *osp.* osphradium; *p.g.* pedal ganglia; *pl.g.* pleural ganglia; *pl.p.c.* pleuro-pedal connective; *pl.pa.c.* pleuro-pallial commissure; *p.a.c.* pallio-abdominal commissures; *sb.g.* subintestinal ganglion; *sp.g.* supra-intestinal ganglion.

mantle nerve from the left pleural ganglion fusing with the branchial nerve emanating from the supra-intestinal or primitively right pallial ganglion, thus forming a nerve loop above the alimentary canal; and by a similar junction having been effected beneath it on the right side of the body between the pallial nerve arising from the right pleuro-pedal connective, but whose fibres probably originate in the right

pleural ganglion and the pallial nerve from the primitively left pallial or sub-intestinal ganglion, the crossing of the pleuro-abdominal commissures having brought these ganglia into close proximity, although prior to it occupying opposite sides of the body.

Zygoneury is an exaggerated development of Dialyneury, in which a much closer approximation or even a fusion takes place on one side of the body only, of the pleural and pallial ganglia, morphologically belonging to opposite sides of the median line, owing to the shortening of the pleuro-pallial commissure and of the anastomosed nerves, whose connection constituted Dialyneury; usually it is the primitively

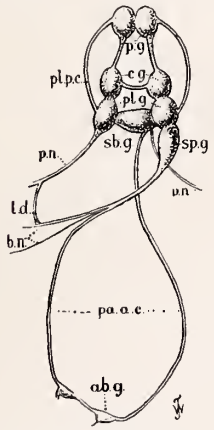


Fig. 439. — The nervous system of *Buccinum undatum* (L.), illustrating Zygoneury to the right, and incidentally Dialyneury to the left (after Pelseneer).

sb.g. subintestinal ganglion fused to the right pleural ganglion and constituting Zygoneury to the right; *sp.g.* supra-intestinal ganglion; *l.d.* nerve joining the pallial nerve from the left pleural ganglion to the branchial nerve emanating from the supra-intestinal ganglion and constituting Dialyneury to the left.

ab.g. abdominal ganglion; *b.n.* branchial nerves; *c.g.* cerebral ganglia; *p.g.* pedal ganglia; *p.n.* pallial nerve; *pl.g.* pleural ganglia; *pl.p.c.* pleuro-pedal connective; *pa.a.c.* pallio-abdominal commissures.

left pallial or sub-intestinal ganglion which becomes closely associated with or actually fused to the right pleural ganglion, and constitutes Zygoneury to the right; more rarely the primitively right pallial or supra-intestinal ganglion is similarly connected to the left pleural ganglion, and is distinguished as Zygoneury to the left.

THE SENSORY ORGANS.

Interspersed among the glandular, ciliated, and simple epithelial cells, which cover the external surface of the mollusk, are a number of elongate or superficially expanded neuro-epithelial cells, known also as Flemming's cells, which often bear one or more sensory hairs at the free end, and vary in number in the various areas, but may be congregated together in certain definite parts of the body, each cell being continued at the base into a nerve fibre, which is connected with the central nervous system. These cells have not

primitively a definite and precise function, and may respond to different stimuli, but when densely aggregated together in restricted areas of the body they form the sensory organs which, by the development of specialized parts adapted to collect and transmit particular forms of stimulation, convey to the mollusk more or less definite impressions of the character of external objects ; thus, the optic nerves are only sensitive to rays of light, and the olfactory nerve to the presence of odours, whereas the less specialized sensibility to tactile impressions is distributed over the entire surface of the body, which is extremely sensitive to the slightest contact.

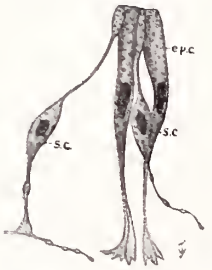


FIG. 440.—Sensory and epithelial cells, showing their arrangement, highly magnified (after Garnault).
ep.c. epithelial cells ; *s.c.* neuro-epithelial or sensory cells.

The OLFACTIVE faculty is undoubtedly possessed by the mollusca, and almost every part of the animal has been suggested, at one time or another, as the seat of this function, but modern investigation favours the view that although the tentacles and the sensory area near the respiratory orifice are the chief seats of this sense, yet the oral cavity in *Helix*, *Limnæa*, and some other genera has also some olfactory power, while the whole soft skin of the animal, which somewhat resembles a pituitary membrane, is probably also more or less sensible to the perception of odours.

In the different genera this sense is more especially concentrated in, and exercised by morphologically distinct regions of the body, which according to their position are termed Osphradia or Rhinophores, the former being more especially adapted to aquatic and the latter to aërial respiration : where both are present, their different degree of functional development is probably in inverse proportion to each other, one being probably in process of development and the other undergoing degeneration.

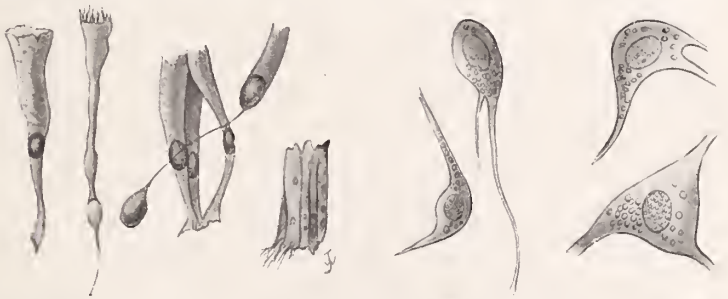
The OSPHRADIUM (ὀσφράδιον, from ὀσφραίνομαι, to smell) or pallial olfactory organ, known as the organ of Lacaze and also as Spengel's organ, is a primitively paired sensory structure, formed by tracts of suitably modified ciliated epithelium, usually innervated from the visceral or pallial ganglia and placed at the outer base of each ctenidium, functioning as an examiner and co-ordinator of the sensations received from the stream of inhalent water which bathes the gills.

The originally paired character of the osphradium is still retained by the Pelecypods and the more archaic Streptoneura, but in the Gastropoda of our fauna the torsion undergone by the body has, in dextral species and individuals, resulted in the atrophy and loss of the osphradium and other organs of the primitively left side and of those of the primitively right side in such forms as are sinistrally coiled.

FIG. 441.—Osphradium or pallial olfactory organ of *Planorbis corneus* (L.), highly magnified (after Felix Bernard).

bl.s. blood sinus; *c.* olfactory pit; *c.t.* connective tissue; *g.c.* olfactory ganglion cells; *s.ep.* olfactive epithelium.

The osphradium seems to be more particularly correlated with an aquatic habit of life and the presence of a branchial cavity, as it is practically absent in terrestrial genera, and in those aquatic forms deficient of a pallial chamber, though still persisting in some species that have comparatively recently relinquished an aquatic life and branchial respiration, but when thus present it always corresponds more or less closely in position with that of the vanished ctenidium, with which it was primitively associated. In its simplest form the



FIGS. 442. 443. 444. 445. 446. 447.

Various forms of cells from the osphradium or olfactory pit of *Limnæa stagnalis* (L.), highly magnified (after Simroth).

Fig. 442.—Goblet cell. Fig. 443.—Ciliated cell. Fig. 444.—Group of cells, one united to a nerve cell by a nerve thread. Fig. 445.—Group of cells with yellow pigmented nuclei and nerve prolongations. Fig. 446.—Olfactory bipolar and Fig. 447. multipolar ganglion cells.

osphradium is merely a localization of suitable epithelial sensory cells, connected with the integument and placed within or near the entrance to the respiratory cavity, upon the course of the branchial nerve, or upon a special osphradial nerve or ganglionic enlargement

derived from it. In some marine Streptoneura the osphradial ridge by specialization acquires bilateral pectinations and, from its resemblance to the gills, was formerly known as the Parabranchia, being supposed to represent the atrophied primitively left ctenidium, but in other groups it may be a simple or bifurcate vibratile pit or invagination, with its special ganglion placed at the bifurcation or at the blind end.

The Rhinophores (ῥίς, ῥῑνος, nose: φέρω, to bear) are the olfactory organs of the head, and in the Stylommatophora are placed in the more elevated epithelium at the apex of the tentacles, a situation which seems to be more especially a characteristic of the terrestrial snails. An olfactory ganglion is placed near the distal end of each

Fig. 448.—Rhinophore or cephalic olfactory organ of *Cyclostoma elegans* (Müll.) × 30 (after Garnault).

cu. cuticle; *olf. ep.* olfactory epithelium; *olf. n.* olfactory nerve with terminal branchlets; *m. t.* muscular and connective tissue with blood sinuses.

Fig. 449.—Isolated olfactory sensory cells from the rhinophore or cephalic olfactory organ of *Cyclostoma elegans* (Müll.), highly magnified (after Garnault).

tentacle and gives origin to numerous fine nervous ramifications, which reach the delicate external epithelium and terminate in numerous superficial olfactory cellules. The olfactory ganglia are connected to special lobes of the cerebral ganglia, and associated with the optic and acoustic nerves which arise from the same lobes.

The Supra-pedal gland has been, and by some authorities is still, regarded as the chief seat of the olfactory sense, owing to its rich innervation and the presence of a number of sensory cells in the lumen of the gland.

The Streptoneura, which are essentially aquatic mollusks, possess the osphradium, usually in the form of a filiform, and often pectinate, ridge, placed within or near the entrance to the respiratory cavity, upon a nervous cord or a small ganglionic enlargement, arising from

the supra-intestinal ganglion, which is the homologue of the right pallial or visceral ganglion of the Euthyneures.

In *Cyclostoma* and other species, which have comparatively recently become adapted to a terrestrial life and aërial respiration, the rhinophores have become developed and acquired functional efficiency and an organization quite similar to those of the Stylommatophora or typical land snails, although the osphradium associated with their primitively aquatic mode of life is also recognizably present, but probably undergoing degeneration.

In some of the more primitive Streptoneura, other sensiferous areas, formed by congregations of sensory cells and bearing sensory setæ are found near the bases of the epipodial tentacles, receiving their innervation from the pedal ganglia.

In the Stylommatophora, although the anterior tentacles possess some degree of olfactory power, this sense is more especially concentrated in the dorsal pair, the bulb-like terminations of which are especially rich in fine club-shaped sense cells, with rods placed amongst specially modified epithelial cells, the somewhat clavate olfactory ganglion in each rhinophore being placed close to the bulbous distal end, and giving rise to several short, thick and divergent nervous branches, whose numerous ramifications form a beautiful and delicate tuft of nervous fibrils, distributed upon a delicate granular membrane beneath the moist integument at the apex of the tentacle. The ganglion varies in volume in correspondence with the keenness or feebleness of the olfactory sense and in some *Hyaliniæ* is scarcely noticeable, while in *Helix pisana* it has four times the thickness of the olfactory nerve.

The osphradium, being an organ more especially adapted to aquatic life, is generally absent in the Stylommatophora ; it is, however, still retained in a feebly-developed state at the lower posterior corner of the lung cavity in *Testacella* and by some Helices. It has also been detected to be present during development in *Limax*.

In the Basommatophora, the tentacles were considered to be the seat of this faculty by Lespes and Moquin-Tandon, the nerves are however not so decidedly concentrated as in the Stylommatophora, but more equally distributed over their whole extent, the superficial surface of the tentacles being increased by elongation in *Planorbis* and by attenuation and dilatation in *Limnæa,* although there is stated to be an olfactory ganglion near the tip, quite removed from the eye,

with which the olfactory sense is so closely associated in the Helices, etc. Lacaze-Duthiers considers the external basal enlargement of the tentacles to also possess olfactory power.

In the *Limnæidæ* the osphradium has persisted after the loss of the gill with which it was primitively associated, and now exists in the form of a rounded epithelial ridge, placed upon or as a vibratile pit, invaginated within a small olfactory ganglion, this olfactory sinus being simple in the sinistral genera *Physa*, *Planorbis*, etc., but bifurcate in the dextral genus *Limnæa*, and, as might be expected, *Planorbis* has retained the osphradium of the originally left side, and the innervation by the left visceral ganglion, while *Limnæa* has retained that of the original right side and receives its nerve supply from the right visceral ganglion but being an aquatic sensory organ, whose rôle is to guard the entrance to the pallial cavity, it has quitted its primitive position inside the mantle chamber and become exterior to it, partly due to the contraction of the pallial opening in the ancestors of the Pulmonates, but mainly because water does not now normally enter the pallial cavity of the *Limnæidæ*. In *Siphonaria*, a marine Basommatophore, in which the water now enters the lung, the osphradium is partially within the cavity.

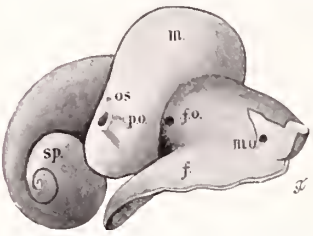


FIG. 450. — *Limnæa peregra* (Müll.) extracted from its shell and the mantle flap turned back to show the position of the osphradium in relation to the pulmonary orifice, etc., × 3. *f.* foot; *f.o.* female aperture; *m*, mantle flap; *m.o.* male aperture; *os.* osphradium; *p.o.* pulmonary orifice; *sp.* spire.

Simroth at one time considered the osphradium to be the medium by which these pulmonate aquatic snails became acquainted with their arrival at the surface of the water for the purpose of respiration.

In the Pelecypoda, Spengel has demonstrated in *Anodonta* and other species a paired osphradial structure richly supplied with nerves, situate upon the roof of the inhalent siphon, near the origin of the branchial nerves, and close to the posterior adductor, analogous in position and structure with the osphradia of the aquatic Gastropods. It is a specially modified crest of epithelium, consisting of a thin layer of elongated sensory cells, placed near to and innervated from the visceral ganglia, but according to Pelseneer the nervous connection is really with the cerebro-pleural ganglia, by means of the cerebro-pleuro-visceral commissures.

In addition to the true osphradia, there have been detected in certain species not within our scope, other sensory organs of probably analogous function, which may exist in the Asiphonated species as a pair of epithelial papillated sensory areas, innervated from the posterior pallial nerve and placed at each side of the anus.

In the Siphonated forms these organs may exist upon the siphonal retractors or at the base of the branchial siphon in the form of papillæ, tentacles, or lamellæ, and receive their innervation from a special siphonal ganglion.

Odours of various kinds are undoubtedly attractive to snails and slugs, which, in all probability, discriminate their food by the aid of the olfactory sense, this faculty in *Arion* and other genera being effectually functional at comparatively great distances, even for isolated objects of restricted size. Moquin-Tandon has recorded that in the Jardin des Plantes, Toulouse, he observed one rainy day two *Limax maximus* crawling from different points towards a decaying apple; he raised the fruit and moved it to the right and afterwards to the left of the animals, but the Limaces unerringly changed their direction in accordance with the altered position of the fruit, never moving in a wrong direction. When the fruit was held above them the tentacles and body were directed towards it and efforts apparently made to find some means of reaching the food.

It has also been well established that snails quickly emerge from their shells when food they like is placed beside them, the odour in these cases being the only available indication of its presence, visual assistance being impossible.

Helix aspersa, as is known, will frequently traverse with much labour broad dusty roads and climb rough walls to reach some favourite food, this being another evidence of the keenness of the olfactory faculty.

In the Pelecypoda the evidences of the exercise of this function are few. Mr. King has, however, recorded the attraction by putrefying flesh of large numbers of *Pisidium pusillum*, which, in a few days' time, were found clustered upon the skull of a fox placed in a small ditch to soak, doubtless feeding upon the minute floating particles of flesh and the organisms developed thereon.

The Exhalation of strong and special odours by the animals of certain genera is probably connected with their season of reproduction and may possibly be of a signalling character, and though, in some cases, doubtless of a protective nature, would seem to imply in

the animals themselves the power to perceive them. Our British *Hyalinia*, especially when irritated or plunged in hot water, emit a strong and pungent smell of garlic, more or less intense according to the species and to the accidental circumstances influencing it, the power culminating in *Hyalinia alliaria*. All *Hyalinia* do not however secrete this unpleasant odour, as at least one foreign species emits a fragrant musky perfume, and has been styled *Hyalinia fragrans* on this account. Certain species of *Clausilia* and *Pupa* have been observed to give out a perceptible spermatic odour, as also does *Aplexa hypnorum* when the animal is crushed. *Helix pomatia* is said to smell strongly of hemlock in the beginning of June, a smell which does not proceed from browsing on the plant, but from an exhalation peculiar to the season of reproduction, while *Unio pictorum* and allied species at the same season have been stated to strongly exhale a caprine or goat-like odour.

The sense of Sight is possessed by the bulk of our native species, either in the larval or adult stage, but it is probable that all our species are, in addition, more or less acutely sensible to the perception of light and shade, owing to the sensitiveness of the neuro-epithelial cellules of their external integument.

It was formerly thought that the mollusca were quite blind, the eye-specks being regarded as merely ornamental spots without any useful function, but their complex structure would appear to indicate greater visual power than they have as yet been actually shown to possess, and in the least specialized forms will at least enable the creatures to discriminate night from day and thus warn them to seek places of safety from their more numerous diurnal enemies.

The visual organs in the various groups are known as Cephalic, Dorsal or Pallial eyes, according as they are developed upon the head region or upon the more exposed portions of the body or mantle, their origin being probably due to the local modification of the external integument through the attraction and accumulation of pigment granules at those parts of the body most exposed to the action of light.

The Cephalic Eyes originate behind the velum and in their primitive form are merely simple cup shaped invaginations of the external epithelium lined with pigmented and retinal cells and rods, such as are still possessed by *Patella* and other archaic species. They were probably originally possessed by all mollusks, and are retained in

various degrees of specialization by almost every Gastropod, and still perceptible during development in the Pelecypods. They differ from the Vertebrate and also from the pallial molluscan eye in the optic nerve being distributed posterior to the retinal rods, which are directed towards the crystalline lens. In the Gastropoda the cephalic eyes are always two in number, usually black or blackish in colour and

Fig. 451.

Fig. 452.

Fig. 453.

Heads of examples of the three chief groups of Gastropods, to show the position of the cephalic eyes.

Fig. 451.—*Vivipara vivipara* (L.), showing the eyes on short pedicels exterior to the tentacles, a position especially characterizing the Streptoneurous species (after Moquin-Tandon).

Fig. 452.—*Limnæa stagnalis* (L.), River Torne, Yorks., showing the eyes at the inner base of the tentacles, as illustrative of the Basommatophora.

Fig. 453.—*Succinea putris* (L.), Christchurch, Hants., × 3, showing the eyes at the tips of the tentacles, as an example of the Stylommatophora.

placed upon or at the base of the tentacles at the anterior part of the body. They are usually more or less spherical, though inclining to an elongate shape in the aquatic species, but their size bears no relation to that of the mollusk, being almost rudimentary in *Testacella* and very large in *Carychium*, but as usual are proportionately larger in the embryo than in the adult.

The Cephalic eyes of any of our species are not appreciably inferior to the highly organized eye of *Helix*, which has a very complicated structure, the Optic nerve which arises from an anterior lobe of the cerebral ganglion being joined with the tentacular nerve, from which it separates at a variable distance from the eye. In *Agriolimax agrestis* and *Testacella haliotidea* this separation takes place quite at the base of the tentacle, but in *Helix aspersa* quite within it. The nerve usually contains ganglion cells and expands into an optic ganglion before reaching and spreading over the rear of the Retina, the part actually sensitive to the impact of light, which occupies the rear of the optic chamber, and is a cuticular formation, originating from the epithelial cells of the base of the invagination and constituted by Retinophores and Retinules, both of which arise from differentiations of normal cells and blend together insensibly in character.

Fig. 454. — Section through partially retracted ommatophore of *Helix aspersa* Müll., × 8, with the retractor removed to show the position of the eye during retraction and the junction within the tentacle of the delicate optic with the larger olfactory nerve

The Retinophores are elongate colourless sensory cells with very contracted free ends, and with their bases joined to and continuous with the nerve prolongations; while the Retinules are pigmented cells with

Fig. 455.

Fig. 456.

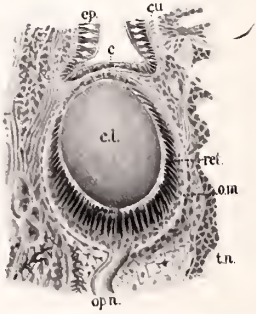


Fig. 457.

Three assumed stages in the evolution from the simple to the more highly organized cephalic eyes of Gastropods, showing the retinal rods directed towards the lens and the distribution behind them of the optic nerve, and also exhibiting different degrees of specialization at which further development has been arrested in certain species.

Fig. 455.—Simple epithelial invagination forming the primitive cephalic eye of *Patella*, highly magnified (after Hilger). *ep.* epithelium; *op.n.* optic nerve; *r.* retina, with superposed retinal rods and a mucoid accumulation, which is assumed to represent the origin of the refractive body.

Fig. 456.—Cephalic eye of *Trochus*, highly magnified (after Hilger), showing the arrestment of development before the formation of the cornea, etc. *ep.* epithelium; *l.* crystalline lens; *op.n.* optic nerve; *r.* retina, with retinal rods.

Fig. 457.—Cephalic eye of *Helix pomatia* L., highly magnified (after Simroth), as exemplifying the degree of organization attained by the eye of the British extra-marine mollusks. *c.* inner cornea; *cu.* cutis; *c.l.* crystalline lens; *ep.* epithelium, becoming thin and transparent and forming the outer cornea; *o.m.* outer membrane or sclera; *op.n.* optic nerve; *ret.* retina; *t.n.* tentacular nerve.

their free extremities very wide, so that they encompass or surround the retinophores, and constitute the pigmented layer, formerly described as the Choroid, but which does not correspond to the pigmented vascular layer known by that name in the Vertebrate eye; in *Cyclostoma elegans* the pigmented retinules are filled by black granules,

Fig. 458.

Fig. 459.

Fig. 458.— Retinophores or sensory cells and Retinules or pigmented cells from the retina of *Cyclostoma elegans* (Müll.), highly magnified, to show their arrangement (after Garnault). *ret.* retinophore; *rs.* retinule.

Fig. 459.—Diverse forms of the Retinophores or sensory cells from the retina of *Cyclostoma elegans* (Müll.), highly magnified (after Garnault).

which, when freed from the cells, have active brownian movements. The Crystalline lens, with the development of which the optic vesicle becomes a true eye and capable of forming a more or less definite image on the retina, is a transparent sphæroidal body of concentric

structure and somewhat gelatinous consistency, secreted by the retinal epithelium and surrounded partially or entirely by a more fluid cuticular substance, the Vitreous body, these refractive parts of the eye being probably primitively represented by a mere accumulation of mucus within the integumental invagination. The transparent outer Cornea is formed by an extension of the outer integument over the optic vesicle and varies in convexity and prominence, while the inner Cornea or pellucida is immediately beneath and formed by the colourless internal wall of the ocular bulb. The Sclerotic is the hard structureless membrane often difficult to separate from the cornea which surrounds and gives to the eye its distinctive form.

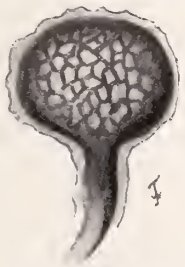


Fig. 460. — Optic bulb of *Helix pomatia* L., after maceration, × 25 (after Simroth), showing the arrangement of the pigmented cells.

By disuse, owing to the adoption of special or peculiar habits of life, the eyes may, as in *Cæcilioides*, become diminished in volume and buried in the integument, or may retain their superficial position and degeneration arise from the loss of the pigmentation.

The Pallial and Dorsal Eyes or Ocelli are secondarily-acquired visual organs, differing totally in many respects from the more primitive cephalic eyes, and conforming in important features to the structure of the eyes in Vertebrates. They are especially developed in the Pelecypoda on the more exposed parts of the mantle margins, owing to the primitive cephalic eyes, temporarily present during development and during the free-swimming larval stage, becoming atrophied and lost, as when overgrown and enclosed by the mantle and shell they are useless. In *Onchidium*, a genus of marine pulmonates, dorsal eyes are developed, in addition to the cephalic eyes, in the forms inhabiting certain districts which are coincident with the range of the *Periophthalmus*, a leaping shore fish, which preys upon them.

In the Pelecypods the pallial eyes have originated upon the nerves arising from the innumerable small ganglia of the marginal pallial plexus, and may be little more than pigmented spots, acutely sensible to light, scattered upon the more exposed parts of the mantle, and, as in *Arca*, may, by their combination in groups, form composite eyes resembling in structure certain simple Arthropodan eyes, each constituent eye or ommatidium being formed of a conical visual cell,

enclosed by six cylindrical pigment cells and a cuticular cornea, with filiform interstitial cells interposed between the ommatidia; or, as in *Pecten*, the pallial eyes by specialization may become of very complicated and elaborate structure, a subepithelial cellular lens which originates from the embryonic ectoderm covering the eye and the optic nerve spreading out around and above the retina, or as in the dorsal eyes of *Onchidium*, piercing the retina posteriorly, the point of entry of the retinal rods forming the "blind spot," as in the Vertebrate

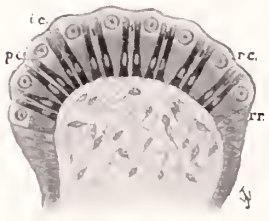


Fig. 461.

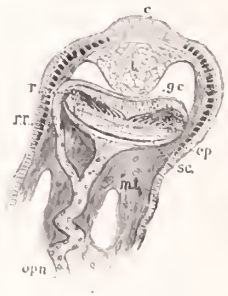


Fig. 462.

Fig. 463.

Sections through the Pallial and Dorsal eyes of *Arca*, *Pecten* and *Onchidium*, to illustrate their differences in organization from that of the cephalic eyes.

Fig. 461.—The composite eye of *Arca barbata*, highly magnified (adapted from Rawitz), showing its complex structure. *i.c.* interstitial cells; *p.c.* pigmented cells; *r.c.* retinal cells, with rod-like bodies; *r.r.* retinal rods.

Fig. 462.—The pallial eye of *Pecten*, highly magnified (after Patten), showing the diffusion of the nerve fibres above the retina. *c.* cornea; *cp.* pigmented epithelium; *g.c.* ganglion cells; *l.* lens; *m.t.* muscular and connective tissue with blood spaces; *op.n.* optic nerve; *r.* retina; *r.r.* retinal rods; *sc.* tapetum, pigmented epithelium and sclerotica.

Fig. 463.—The dorsal eye of *Onchidium verruculatum*, highly magnified (after Semper), showing the piercing of the retina by the optic nerve and the consequent formation of the "blind spot" and the distribution of the nerve fibres above the retina. *c.* cornea; *l.* lens; *op.n.* optic nerve; *p.* pigment layer; *r.* retina.

eye, the resemblance to which and the divergence from the molluscan cephalic eye being, in both forms, further emphasized by the visual rods being turned towards the body away from the light, and the retina generally being reversed in its arrangement to that obtaining in the cephalic eye.

Pallial eyes, with few exceptions, appear to be especially developed amongst littoral species, and the more recent relinquishment by *Dreissensia*, in comparison with the Naiads and other more ancient fluviatile forms, of a littoral for a fluviatile life has been held to account for the more perceptible presence of the pigmented visual cells with highly refractive cuticle, which are concentrated on the siphonal margin of that species.

In addition to and independent of the more or less definite iconoptic vision by the more specialized eyes of the mollusk, the integument of many species also possesses a certain degree of Dermatoptic

power, the various species, according to their habits, exhibiting a more or less striking response to sudden illumination or shading, the reaction being more or less apparent in accordance with the intensity of the light or depth of the shadow, this perceptive power being due to the sensibility of the peripheral neuro-epithelial cells; the Rev. J. E. Tenison-Woods, however, affirms the presence in the mollusca generally of a multiplicity of minute eyes, corresponding to the Aesthetes of the Isopleura, these organs being said to exist, not only on the mantle-lobes of the animal, but even upon the opercula and the outer surface of the shell itself, while in addition there are large isolated eyes within the shell substance.

Such species as markedly react to light are distinguished as Photoptic, those which are strikingly affected by shade as Skioptic, while the species which perceptibly respond to both light and shade are known as Photoskioptic.

According to Nagel, *Helix pomatia* and *Helix hortensis*, if left for a time undisturbed, are acutely skioptic, but *Helix arbustorum* is less markedly affected, especially if the animal be a darkly pigmented one, while the slugs generally are said to be only slightly responsive, although Mr. E. J. Lowe, who had charge of the "Himalaya Eclipse Expedition" of 1860, stationed near Santander in Spain, has recorded his observation there of the intense skioptic sensibility of *Arion ater* and also of *Helix pisana*, as shown by their almost immediate response to the advent of the gloom at 3 p.m., due to the obscuration of the sun's disc, both species being observed to be actively moving about as at dusk, even before the eclipse became total.

Unio pictorum, *Unio margaritifer*, and other species are photo-skioptic, for, in addition to a perception of a sudden accession of light, they are also keenly responsive to sudden shading, as is evidenced by the rapid withdrawal of the mantle and closure of the shell, the latter species immediately closing its shell if the sun becomes overcast, the water muddied or even if a boat passes above at a scarcely perceptible speed.

In the Streptoneures the eyes are elevated upon slightly contractile special eye stalks or ommatophores, external to and more or less closely fused with the tentacle, and not invaginable. In some of the more archaic marine Rhipidoglossa the eye is not always closed by the cornea, but is merely a simple tegumentary invagination, lined with sensory and pigmented epithelium.

In the Stylommatophora the eyes though in the adult borne obliquely at the extremity of the upper or dorsal tentacles, are lateral during development, only acquiring the apical position at a later period, a situation which enables them to be readily protruded or invaginated within the tentacle for protection, but they are only functional when the tentacle is fully protruded. In this invagination or retraction the relative position of the crystalline lens and the ocular bulb are reversed, the retractor muscle causing the lens to descend the tentacular tube in advance of the body of the eye. The genus *Vertigo*, in which, though bitentaculate, the eyes are borne at the tip of the tentacles, is also Stylommatophorous.

In the Basommatophora the eyes are sessile and placed at the internal base of the tentacles, and often contain a blood space between the outer cornea and inner cornea or pellucida. They have generally very feeble ocular powers, for although Stiebel considers *Limnæa stagnalis* to be better endowed in this respect than the Helices, Lespes has shown that the allied genus *Planorbis* only perceive objects when in very close proximity to their visual organs.

In the Pelecypoda, although the cephalic eyes are absent in the adult stage, they are retained by *Dreissensia* throughout the free-swimming larval stage, and are transitorily present in other species at an early stage of their development. In compensation for the subsequent loss of these cephalic visual organs, primarily due to their enclosure within the valves of the shell, numerous pallial eyes are in process of development along the mantle margins, which are more or less acutely sensible to light and shade.

All our land and freshwater mollusca are unquestionably myopic: they do not perceive the ultra violet rays, but are especially adapted for vision in dim crepuscular light, as exposure to bright sunlight appears to have a dazzling or blinding effect upon them. Most Gastropods shun the full noon-day glare, and seldom voluntarily leave their retreats except during twilight or total darkness. The aquatic Pulmonates have very feeble ocular powers and cannot discriminate the form of objects even in immediate proximity to their eyes, but the terrestrial species have a much keener perception, experiment demonstrating that in a dim light Helices perceive large and bulky objects at a distance of six centimetres, but in a bright light their power of vision is much impaired, and this distance is so greatly reduced that it may not even exceed four millimetres. *Vivipara*

contecta is comparatively long sighted, perceiving objects at a distance of thirty centimetres from the eye, or if the mollusk be crawling in the gloom the sudden advent of a bright light at a greater distance will cause it to at once retire within its shell. *Cyclostoma elegans* can also distinguish the hand of the observer when within eight inches or twenty centimetres, and abruptly contracts within and closes the shell on its nearer approach.

The Auditory or Equilibrating organs were quite unknown in the mollusca prior to their discovery in the Cephalopoda by the celebrated anatomist, John Hunter. In 1838 Siebold detected the same organ in *Anodonta*, *Unio*, and other Pelecypods, and afterwards in many Gastropods, and its resemblance, in some species, to the auditory organs of certain fish-embryos strengthens the generalization that the fully developed organs of the lower animals may often represent those of the higher forms of life in an early stage of their development.

The sense of hearing in mollusks cannot, however, be very acute, as the so-called auditory organs, when present, are reduced to their simplest expression, two small closed sacs, termed otocysts, filled

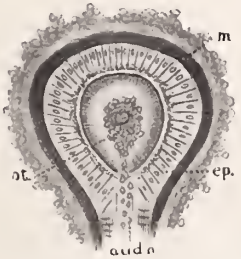


Fig. 464. — Section of the otocyst of *Neritina fluviatilis* (L.), highly magnified (after Boll).
aud.n. otocystic or auditory nerve; *ep.* epithelium; *ot.* otoconia; *m.* muscular layer with connective tissue.

Fig. 465.—Otocyst of *Anodonta cygnea* (L.), showing the cellular walls, the enclosed otolith, and more especially the exterior distribution of the otocystic nerve, highly magnified (after Simroth).

with a limpid fluid, and each holding in suspension one or many crystalline and sometimes coloured calcareous concretions, which vary in size, form and chemical constitution in the different species. The epithelial walls which secrete the endolymph or humour filling the sac, consist of ciliated and sensory cells, the latter with fine rod-like processes connected directly with the auditory nerves, whose fibres are distributed over the walls of the vesicle; while the ciliated cells by their action create the incessant quivering and oscillation of the otoliths or otoconia, their concussion or contact with the longer

sensory hairs upon the walls of the sac inducing or leading to the suitable reflex actions of the animal.

Although termed auditory organs, they are probably only sensitive in a very limited degree to sound audible to human ears, but have a

Fig. 466.—Portion of the otocyst of *Spherium corneum* (L.), highly magnified (after Simroth), showing the otolith, *ot.*, in contact with the sensory hairs.

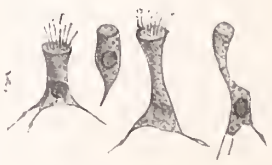


Fig. 467. — Terminal nerve cells from the walls of the otocyst of *Cyclostoma elegans* (Müll.), highly magnified (after Garnault).

much keener perception of any disturbance of the inhabited medium or of the surface to which the foot may be applied. Their chief function is undoubtedly to regulate the orientation and preserve the equilibrium of the body by aiding in the perception of the horizontal position during locomotion, probably by reflex muscular action, induced by the varying movements of the otoliths upon the sensory nerve-endings. This function is the more likely to be the predominant one, as this organ becomes atrophied in the adult stage of the fixed forms, such as *Dreissensia*, though present in the free swimming early stages of growth.

The otocysts are most highly developed in the active forms, and in the reptant species are usually found near to or actually in contact with the pedal or locomotory ganglia, but in the natant forms they tend to approach the cerebral ganglia, from which centre they receive their innervation. In our Gastropods they vary in the position they occupy, being comparatively remote from the pedal ganglia in *Cyclostoma* ; actually placed upon or imbedded within their posterior outer surface, as in the Stylommatophora ; or, as in *Neritina*, may be close to, yet quite distinct from, the ganglionic mass.

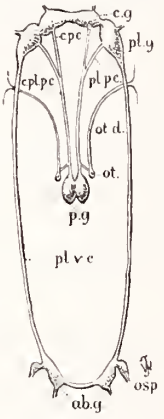


Fig. 468. — Diagram of the nervous system of *Nucula*, showing the open canal of invagination from the otocysts to the exterior, and incidentally the still separate cerebral and pleural ganglia and their connectives (after Pelseneer).

ot. otocyst; *ot.d.* otocystic duct; *ab.g.* combined pallial and abdominal ganglia; *c.g.* cerebral ganglia; *c.p.c.* cerebro-pedal connectives; *c.pl.p.c.* cerebro-pleuro-pedal connective; *osp.* osphradium; *p.g.* pedal ganglia; *pl.g.* pleural ganglia; *pl.p.c.* pleuro-pedal connective; *pl.v.c.* pleuro-visceral commissures.

The otocysts originate in the embryo as simple paired invaginations of the outer epithelium of the foot, the canal of invagination or Kölliker's canal, as it is termed in the Cephalopods, persisting only in the adult *Nucula* and other primitive Pelecypods, and opening externally at the anterior end of the foot, the otoconia being composed of grains of sand or other extraneous particles.

The calcareous concretions or "hearing stones" contained within the sacs are, like the calcareous basis of the external shell, usually composed of that form of carbonate of lime termed Aragonite, and directly originate from the cells of the sac.

They may be classified for the purposes of study as Otoliths and Otoconia, according to the number and character of the concretions contained in the cysts.

The Otoliths (οὖς, ear; λιθος, stone) are comparatively large, often solid, and more or less spherical concretions, usually distinguishable from the calcareous spherical granules found in other parts of the body or mantle by their concentric structure and radial striation; they always exist singly within the cysts, and do not increase in number with the age of the animal.

Fig. 469.—Otolith from the otocyst of *Sphærium corneum* (L.), highly magnified (after Simroth).

The Otoconia (οὖς, ear; κονία, dust) are smaller, more numerous, and more variable in shape than the otoliths, and may be of a simple or compound form; the simple form embraces all otoconia with a regular and simple outline, as those characterizing *Hyalinia* and other genera; the compound forms are distinguished by distinct and usually symmetrical divisions or segments, each showing a minute central area, the demarcation into two or four divisions predominating,

Figs. 470. 471. 472. 473. 474. 475. 476. 477. 478. 479. 480. 481.

Simple and compound otoconia from the otocysts of various species of British Euthyneurous mollusca to show some of the differences in form, highly magnified (after Schmidt).

Figs. 470—472 represent the prevailing forms in the Stylommatophora generally. Fig. 473 more particularly belongs to the Basommatophora. Fig. 474 is more especially found in *Hyalinia*. Figs. 475, 476 are from *Helix pomatia*, but these peculiar forms are only occasionally found and are also not confined to that species. Figs. 477–480 are similarly from *Helix hortensis*, Fig. 480 being an end view of Fig. 479, and Fig. 481 is from *Limax cinereo-niger*.

while the partition into three, five or six segments is less frequent. The number in each cyst also increases with the age of the animal, in an embryo of *Limnæa stagnalis* Siebold counted only fifteen of

these concretions, in one still younger Wagner observed only nine or ten, and Pouchet found in another example but seven, though the adult animal usually possesses more than a hundred. The cysts also do not always contain an equal number of otoconia, nor are they exactly uniform in size and shape, even in the same sac.

The otolith, which is the primitive form in which these concretions first arise during the embryonal development of all our mollusks, is still retained by and more particularly characterizes those genera and species of Streptoneura and Pelecypoda, which in many other respects are amongst our most highly specialized forms, whereas the more archaic genera of these groups and the Euthyneura lose the otolith present during their embryonal life and acquire otoconia.

The otocysts are always more easily examined in the immature than in the adult animal, even in the smaller species, as the whole body can be pressed between the glass slips and the action and movements of the otoconia studied for fifteen minutes or more before they finally cease. In the Naiads this organ is much more difficult of examination and study.

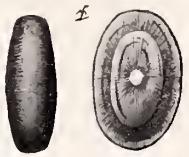
In the Streptoneures, the otocysts are not usually so intimately connected with the pedal ganglia as in the Euthyneures, and, as in the highly specialized *Cyclostoma elegans*, may retain the primitive arrangement of a single large spherical otolith in each cyst, which almost fills the whole vesicle, and in which the concentric lines of accretion or junction predominate, although radial striation is also present, as when crushed it invariably breaks into five pieces. Some species which are, however, otherwise less highly specialized have an exceedingly large number of otoconia, as *Neritina fluviatilis*: those of *Valvata* are quite like those of the Helices, being oval and sometimes angulated at the end, with a yellow central area and a darker nucleus, while certain forms habitually possess an otolith and otoconia in each cyst.

FIG. 482. — Otolith from the otocyst of *Cyclostoma elegans* (Müll.), highly magnified (after Garnault), showing its spherical form, distinct concentric structure and radiate striation.

In the Euthyneures the otocysts are usually placed upon or actually imbedded in the pedal ganglia, the free side being usually more convex than the one attached to the ganglia. They contain numerous otoconia, which though generally more or less oval in shape, with minute central area, yet often show considerable variety of out-

line, the otoconia of the Stylommatophora being usually of a broadly oval form, while those of the Basommatophora are more lenticular

FIG. 483.



FIGS. 484. 485.

Fig. 483. — Underside of the pedal ganglia of *Hyalinia alliaria* (Miller), highly magnified, from Redcar, collected by Mr. Baker Hudson, showing the position of the otocysts upon them. *ot.* otocyst ; *c.c.* cerebro-pedal connective.

Fig. 484 side view and Fig. 485 front view of otoconia from otocyst of *Helix pomatia* L., showing the central nucleus and radiate striation, highly magnified (after Leydig).

in character. The otocystic nerve to each sac is a delicate fibril lying between the cerebro-pedal and the cerebro-pleural connectives of their respective sides and arising from the cerebral ganglia.

In Pelecypods, although the more archaic genera still retain the canal of invagination communicating with the exterior, yet in the adults of our forms the otocysts have become closed and contain only a single otolith in each sac, that of *Sphærium* being a flattened sphere, with radial striation, much smaller in size than the cyst containing it, though other species not members of our fauna may possess a number of otoconia in each sac, or an otolith may be found with otoconia. In the fixed forms, as *Dreissensia*, the otocysts are wanting in the adult stage, though present during development.

FIG. 486. — Otolith from the otocyst of *Sphærium corneum* (L.), highly magnified (after Simroth), showing its oval form, strong radial striation and peculiar nuclear space.

The auditory nerves are closely joined with the cerebro-pleuro-pedal connectives, although their fibres arise from the cerebral centre.

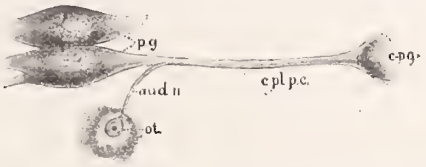


FIG. 487. — Otocyst of left side of *Anodonta*, showing its close connection with the pedal ganglia and the innervation from the cerebro-pleural ganglion, enlarged (after Simroth).

aud.n. otocystic or auditory nerve ; *c.p.g.* cerebro-pleural ganglion ; *c.pl.p.c.* cerebro-pleuro-pedal connective ; *ot.* left otocyst, with otolith ; *p.g.* pedal ganglia.

Generally speaking the auditory organs of the Unionidæ and the Helicidæ form the ends of a series which the other groups unite by intermediate gradations. Some Streptoneures show by their otoliths more affinity to the Pelecypods, while others approach the Stylommatophora.

Sound is said to be produced or emitted by certain foreign mollusks, and *Helix aperta*, a reputed British species, is stated to emit a distinctly audible cry when disturbed, but our native species are not known to emit any sound whatever, except perhaps the audible snap or click which may be heard when an aquatic pulmonate, as *Limnæa*, opens its pulmonary aperture for respiration upon reaching the surface of the water; pulmonate mollusks generally when suddenly alarmed may however by the spasmodic contraction of their bodies and the consequent forcible expulsion of the air from the mantle cavity, produce a perceptible noise, varying somewhat in character according to the force of the contraction and the quantity of mucus accumulated around the respiratory orifice.

What has been called the "Music of Snails" is created by the crawling of the animal on a pane of glass or other suitable substance, but the sound thus produced is a purely mechanical effect and in no sense the voice of the animal—it may be easily imitated by drawing a moist finger along the edge of a wine glass. This sound, which resembles that of an Æolian harp, is usually only heard at dusk or during the night: and the source of the mysterious sound being frequently unsuspected it has often caused a feeling of superstitious dread and forms the basis of an interesting story by Mrs. Bowdich.

The Gustatory sense is doubtless possessed by the Gastropoda, as is evidenced by the predilection of different species for special foods. This faculty probably has its location within or about the buccal cavity, as the tongue being closely beset with hard chitinous denticles, necessary for the rasping and comminution of food does not appear to be a suitable organ for the development of this special sense.

The multilobular dorsal and lateral lips, which constitute the organ of Semper, are probably the seat of the gustatory sense, each lobe being furnished with a small ganglion placed beneath a deep epithelium with a thick cuticle and connected with a branch from the anterior tentacular nerve.

In the Streptoneura the organs of Semper are not developed, but Garnault has detected within the buccal cavity of *Cyclostoma elegans* a number of nerve cells beneath a thick cuticle, some terminated by a delicate filament, which, although somewhat similar in general character to tactile cells, he considers may have a gustatory function.

Fig. 488.—Gustatory cellule from the wall of the buccal cavity of *Cyclostoma elegans* (Müll.), highly magnified (after Garnault).

In the Euthyneura the organs of Semper, although especially developed in the *Arionidæ* and *Limacidæ*, are also present in the Stylommatophora generally, the lateral lobes receiving their innervation from the cerebral ganglia, and the dorsal lobes, according to Hanitsch, receiving two small nerves from the buccal ganglia; each lobe possesses a small ganglion composed of small spherical ganglion cells, such as are found in the more specialized sensory regions of the

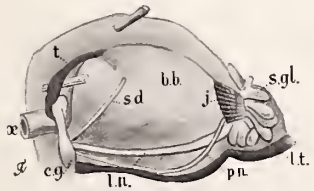


FIG. 489. — Side view of buccal mass of *Limax cinereo-niger* Wolf, × 2, showing Semper's organ (after Sochaczewer).

b.b. buccal bulb; *c.g.* cerebral ganglia; *j.* jaw; *l.n.* labial nerve; *l.t.* lower tentacles; *œ.* œsophagus; *p.n.* nerve piercing beneath side muscles of pharynx; *s.d.* salivary ducts *s.gl.* Semper's organ; *t.* tentacle.

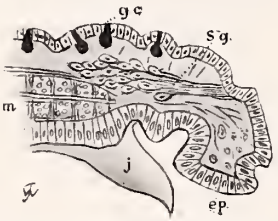


FIG. 490. — Longitudinal section through head of *Agriolimax agrestis* (L.), × 20, showing Semper's glands, gland cells and muscles (after Hanitsch).

ep. epithelium; *g.c.* gland cells; *j.* jaw; *m.* muscle bundles; *s.g.* glands of the organ of Semper, showing their unicellular character and independent ducts.

cerebral ganglia. The epithelium of these special regions is exceptionally thick, as in other sensory areas, and each lobe is moistened by a very fluid secretion from the cluster of somewhat pyriform cells they contain, each cell being furnished with a delicate duct with outlet upon special papillæ placed above the lateral lips at each side of the mouth.

The Basommatophora, although possessing labial ganglia of homologous nature to those of the Stylommatophora, have not the distinctly lobulated lips characteristic of Semper's organ.

The presence of the unicellular glands, whose secretions impart the moistness to the gustatory tissues, has induced some observers to regard Semper's organ as a buccal salivary gland, homologous with the anterior salivary glands found in certain other groups of mollusks.

Simroth is of opinion that the sense of taste is concentrated in the front of the buccal cavity in land shells, but he has not detected this specialized region in aquatic forms, and concludes the sense is in them more diffused over the whole outer surface of the body.

In the Pelecypoda the faculty is hardly developed, but may be exercised by the internal surface of the labial tentacles, which are richly innervated and act as guards to the mouth, though little discrimination appears to be exercised in selecting food, almost anything small enough to enter the mouth being swallowed.

The TACTILE sense is well developed in the mollusca, being resident in all parts of the external skin, which is very soft and moist and acutely sensitive to the slightest contact. This faculty is especially exercised by externally expanded neuro-epithelial cells bearing tufts of sensory hairs and by long and fusiform nucleated cells, which may be prolonged externally into one or more fine setiform sensitive processes, and internally are directly continuous with the nerve fibrils, these cells being most strongly and numerously developed on the most prominent or exposed parts of the body naturally functioning as tactile organs.

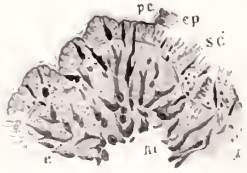


FIG. 491.—Section through the anterior tentacle of *Helix pomatia* L., to show the peripheral tactile cells and general structure, highly magnified (after Flemming).

s.c. sensory cells; *ep.* epithelium; *p.c.* pigment; *n.c.* large nucleated cells; *c.* transverse section through muscles.

In the Gastropoda this sense, though diffused generally over the surface of the body, is most actively exercised by the anterior tentacles and labial lobes, which are possessed of the most delicate susceptibility to contact with external objects.

FIG. 492.

FIG. 493.

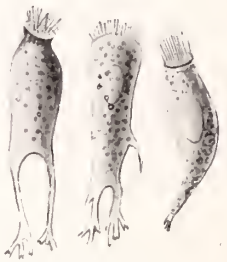


FIG. 494.

Fig. 492.—Afferent nerve and connected afferent ganglion cell, showing its tactile terminations within the external epithelium, × 600 (modified after Boas).

Fig. 493.— Terminal nerve cells and Fig. 491 Epithelial ciliated cells from the tentacle of *Vivipara vivipara* (L.), highly magnified (after Simroth).

In the Pelecypoda the tactile sense cells are distributed over the surface of the body and mantle. The tip of the foot seems especially sensitive and is probably the most effective organ of touch. The papillary processes of the siphons and the mantle margins generally are exquisitely sensitive to tactile impressions, as are the labial tentacles, but the latter are perhaps scarcely organs of touch in the sense intended here.

FIG. 495. — Tentacles of the branchial siphon of *Anodonta cygnea* (L.), × 10 (after Moquin-Tandon).

ALIMENTARY SYSTEM.

The Alimentary or digestive system is well developed in the mollusca, and may be described as a long tube of variable width, convoluted within, but attached by strands of connective tissue to the walls of the primary body cavity or cœlom, and which, in the last or rectal tract of its course, may, in certain groups, traverse the pericardium or secondary body cavity, and sometimes even pass through the ventricle of the heart also, performing different functions in the various portions of its tract or course, all of which have for their objects the extraction of nourishment from the ingested food and its assimilation by the animal for the growth or reparation of its various organs or tissues and the subsequent excretion from the body of waste or hurtful substances..

The whole enteric tract may be conveniently divided into three regions, an anterior, a median and a terminal portion, according to the position and chief function of its various parts.

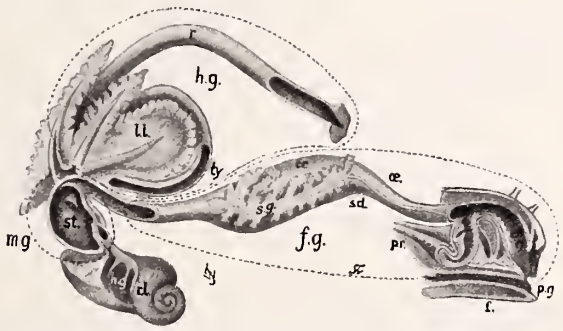


FIG. 496.—Alimentary canal of *Helix aspersa* (Müll.), showing the proposed regional division of its tracts (modified after Howes).

f.g. fore-gut or anterior region of the alimentary tract; *m.g.* mid-gut or stomachal region and *h.g.* hind-gut or intestinal region.

b.c. buccal cavity, showing radula, radula sac and jaw; *cr.* crop; *f.* foot; *h.g.* hermaphrodite gland or ovotestis; *l.l.* anterior lobe of liver; *œ.* œsophagus; *p.g.* pedal gland; *ph.r.* pharyngeal or buccal retractor; *r.* rectum; *r.l.* posterior lobe of liver; *s.d.* salivary duct; *s.g.* salivary glands; *st.* stomach; *ty.* typhlosole.

The Anterior region of the alimentary canal or fore-gut is of ectodermic origin and has an ingestive and comminatory function. It comprises the buccal bulb, with its specialized developments, and the œsophagus or gullet.

The Median or digestive portion of the tract is of endodermic origin and constituted chiefly by the stomach, a dilatation or enlargement of the mid-gut, which in some species contains a chitinous or cartilaginous rod and, with a considerable part of the hind-gut, is

closely surrounded by or imbedded within the large and multilobed liver or digestive gland, which yields a digestive ferment. Sometimes there are several noticeable dilatations in this region, the most anterior of which may function as a crop and others as grinding gizzards for the more effective trituration of the food before arriving at the true stomach or digestive sac.

The Terminal and post-median part or hind-gut comprises the intestinal tract beyond the stomach, which, though much longer than the body containing it, is not, as might be rashly supposed by the uninitiated, indiscriminately coiled within the cavity without any particular or definite arrangement of its often long and numerous tracts, for each species, and more especially those of phytophagous or omnivorous habit, exhibits the most intricate, yet marvellously regular convolutions, the peculiarities of which are so markedly special to each species that many forms can be identified by this

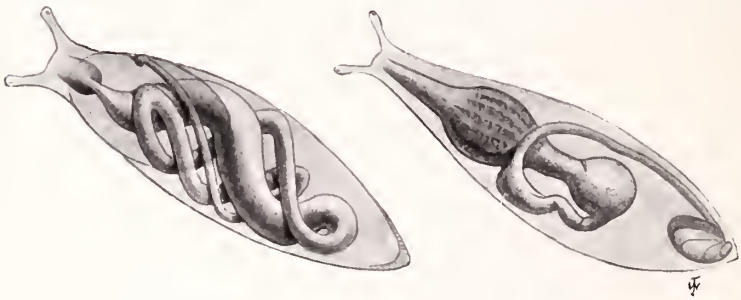


FIG. 497. FIG. 498.

Fig. 497.—Alimentary tract of *Arion hortensis* Fér., × 4, Horsforth, near Leeds, showing the complex intestinal convolutions of an omnivorous species.

Fig. 498.—Alimentary tract of *Testacella haliotidea* Drap., × 2, Horsham, Sussex, collected by Mr. T. S. Hillman, and showing the simple intestinal coiling of a predacious species.

feature alone. The intestinal canal of the strictly predaceous species has always a much simpler and shorter course, but is equally adapted to the nature of the food upon which the creature naturally subsists.

This portion of the alimentary tract has principally an absorptive and excretory function, although intestinal digestion is also carried on along the greater part of its course. It terminates at the anus, which is of ectodermic origin and primitively placed at the posterior end of the body, but in the Anisopleurous Gastropods the torsion of the visceral sac, due to the development of a heavy univalve shell, has, generally speaking, transferred the orifice towards the front, with the respiratory and other apertures with which it is usually associated.

The Stomodeum (*στόμα*, mouth ; *ὁδαῖος*, belonging to a way) or anterior region of the alimentary tract, which comprises the mouth with its related parts and also the œsophagus, is always placed at the anterior end of the body, and in some forms originates as a simple epiblastic invagination of the body-wall of the embryo, which meets with and opens into the mesenteron or median part of the alimentary canal ; sometimes, however, it is formed by the persistence of the blastopore, or orifice of embryonal invagination formed during the gastrula stage of development.

In the Gastropoda the oral aperture is surrounded by variously shaped lips which open into the buccal cavity or pharynx, whose walls, especially ventrally and laterally, are formed by thick longitudinal and annular muscular layers constituting the buccal bulb, which in the more primitive mollusk was placed behind the cerebro-pedal nerve collar, but in the more specialized forms is now in front of it.

The buccal bulb is protruded or retracted by means of special muscles, which, according to their function, are distinguished as Protractors or Retractors respectively.

In the Streptoneura, Garnault has studied their arrangement in *Cyclostoma elegans*, and has described the protrusion of the buccal mass as mainly due to the contraction of the powerful lateral protractors, which arise from the smaller segments of the mandibles and are attached to the external integument near the oral aperture ; these are supplemented by longitudinal muscles within the walls of the buccal bulb.

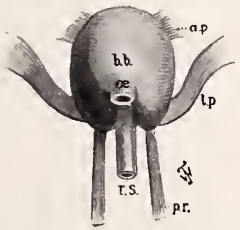


Fig. 499.— Buccal bulb of *Cyclostoma elegans* (Müll.), × 10, showing its chief retractor and protractor muscles (after Garnault).

a.p. anterior protractors ; *b.b.* buccal bulb ; *l.p.* lateral protractor muscles ; *œ.* œsophagus ; *p.r.* pharyngeal or buccal retractors ; *r.s.* radula sac.

The retraction is chiefly effected by two long paired muscles affixed to the larger jaws, which pass somewhat divergently backwards through the œsophageal ring, and mingle with and become lost amongst the pedal strands of the columellar muscle.

In the Euthyneura the protractors of the buccal mass are several small muscular bands attached to the buccal bulb and to the anterior walls of the head region. The retraction is chiefly performed by a branch or branches usually arising from the columellar muscle, which are attached to the ventral and lateral surfaces of the bulb and exhibit much interesting variation in the different species.

The entrance to the buccal cavity is furnished with certain hard cuticular formations, known as the jaws and odontophore, which are distinctly connected together by a partially chitinous membrane, the presence of which can be clearly demonstrated when the caustic solution used in the preparatory process is not too strong.

The mandibles or jaws consist of one or more variously arranged hard chitinous structures, more or less encompassing the oral aperture, while the radula, or odontophore, is a linguiform cartilaginous cushion, which occupies the floor of the mouth cavity, and is beset with numerous hard recurved denticles, serving conjointly with the mandibles for the prehension and comminution of food, thus facilitating the effective action of the digestive fluids of the stomach and also of the secretions from the salivary glands, whose ducts open into the buccal cavity.

FIG. 500. — Longitudinal section through the buccal bulb of a Streptoneure (after Lankester) showing the disposition of the teeth and jaws and the organs of the head generally.

b.c. buccal cavity; *h.c.* head cavity; *j.* lateral mandible or jaw; *l.c.* lingual cartilage; *m.* mouth; *œ.* œsophagus; *p.m.* lingual protractors, posteriorly to them are the retractors; *r.* radula or odontophore; *r.s.* radula sac; *s.* sinus behind the radular sheath; *v.m.* ventral retractor muscles of the buccal mass.

The interior of the buccal cavity generally is lined by cylindrical epithelial cells, overlaid by a thick cuticle, but the roof is covered with a thin but strong and partially chitinous membrane or palatal plate, connected anteriorly with the cutting edge of the monognathous jaw, and overlaying a thick stratum of complexly arranged muscle fibres, having a longitudinal, transverse and dorso-ventral direction, which would appear to confer upon the upper jaw great freedom of motion in various directions.

In the Pelecypoda generally there is practically no pharyngeal specialization, on account of their mode of life not necessitating the active search for food, which consists of minute particles or organisms, not needing mastication, brought in by the inhalent current which their ciliary apparatus perpetually excites; they do not, therefore, possess the accessory and prehensile organs which characterize the Gastropoda, as the oral aperture opens directly into the œsophagus, although some of the more archaic Pelecypods still retain a buccal cavity with two small and laterally symmetrical glandular sacs, which perhaps represent the salivary glands of the Gastropods.

The Mandibles or Jaws are solid cuticular chitinous thickenings, with acute or dentated edges, placed at the anterior part of the buccal cavity; they are almost universally present in the Gastropoda, serving chiefly as prehensile organs for the purpose of seizing or biting off particles of food, and the modifications to which they are subject are most readily appreciated if, as suggested by Lang, they are considered as originating from a circlet of jaws surrounding the entrance to the oral cavity; such as are still possessed by *Umbrella*, *Tylodina* and other Opisthobranchs, and of which special parts have been retained by the various genera, specialization being evidenced by an increasing simplicity and by the reduction in number of the primitively numerous separate parts, owing to the atrophy and loss of certain of the segments and the more or less complete and differing modes of fusion of the parts retained.

The muscular arrangements for the efficient action of the mandibles in the pleurognathous species have been studied, in *Cyclostoma*, by Garnault, who finds that, although the mandibular muscles are to some extent complicated with those actuating the radula and buccal bulb generally, yet there are several distinct muscles directly concerned in their movements, the principal being a powerful transverse muscular band, attached by each end to the external sides of, and connecting together the larger jaws, which by its contraction are brought into close apposition above the radula, the succeeding and alternating separation or re-opening of the jaws being due to the relaxation of the transverse convergent or approximating muscle and the simultaneous contraction of the lateral divaricators.

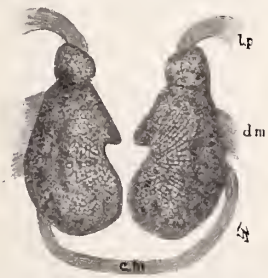


Fig. 501. — Mandibles of *Cyclostoma elegans* (Müll.), × 10, showing their principal actuating muscles (modified after Garnault).

c.m. approximating or convergent muscle; *d.m.* lateral divaricator muscles; *l.p.* lateral protractor muscles.

Though not an invariable rule, it is usual amongst our species for a definite type of jaw to be associated with an odontophore of a certain character, thus the oxygnath jaw of *Hyalinia* is usually correlated with aculeate marginal teeth, which imply a carnivorous tendency; while the strongly ribbed odontognathous jaw is generally found with quadrate and minutely cusped marginals, which are usually held to indicate a preference for vegetable foods.

Our Gastropoda may be conveniently grouped for study as Agnatha and Gnathophora, according as they do or do not possess this buccal armature.

The AGNATHA (*a*, without: γνάθος, jaw) embrace those species entirely destitute of definite or distinct jaws, and are limited in this country to the species of the genus *Testacella*, although, even in that group, the upper or dorsal mandible is represented by an indistinct chitinous thickening.

The GNATHOPHORA (γνάθος, jaw; φέρω, to bear), or jaw bearers, exhibit great diversity in the character and disposition of their mandibular apparatus and, in accordance with the number of their constituent parts, may be conveniently divided into five principal groups or sections, distinguished as Polyplacognatha, Tetragnatha, Dignatha, Trignatha, and Monognatha, although the peculiarities characterizing these divisions, like those separating all other groups, are not sharply marked, but are more or less insensibly blended together by intermediate forms and thus really indicate successive and divergent or, probably in some cases, convergent stages in their progress of specialization.

The POLYPLACOGNATHA (πολύς, many; πλάξ, a plate or piece; γνάθος, jaw) embrace the groups *Sphyradium* and *Punctum*, the former instituted for the reception of *Vertigo edentula* and the latter for *Helix minutissima* of Lea, a form apparently synonymous with our *Helix pygmæa*, all of which agree in possessing the remarkable peculiarity of segmented or composite and nearly circumoral mandibles, composed of a number of somewhat quadrate plates, each formed by long chitinous fibres extending as a fringe beyond their sharp free edges. The plates, though overlapping each other laterally, are distinctly separated medially, all however being slightly connected together by a delicate membrane.

FIG. 502. — Segmented or primitive Polyplacognathous mandibles from *Helix pygmæa* Drap., highly magnified (after Schacko).

At the present time *Helix pygmæa* and *Vertigo edentula* are the only species in this country actually known to posssess this remarkable type of jaw, *Helix rupestris*, which, on strictly testaceological grounds, is apparently so closely allied to *Helix pygmæa*, being a decidedly monognathous species.

The polyplacognathous or composite jaw is an excessively ancient and primitive type, probably especially characteristic of a once almost universally dispersed and more uniform molluscan fauna than any existing at the precent day.

This type of jaw is, however, still retained by a limited number of holarctic species and by *Laoma*, a helicoid genus inhabiting the Southern Hemisphere, these few species at the present time probably solely constituting the now widely scattered and isolated remnants of this ancient fauna, in whose surviving members the specialization of the buccal armature has become arrested and has therefore lagged more or less behind that of the other organs of the body.

The Pleurognathous species embrace the quadrimaxillate and bimaxillate forms and practically includes all our Streptoneures; the paired lateral chitinous jaws, though usually distinctly separated, are in *Lamellaria* and other marine species manifestly fused together dorsally, forming a single piece. They are thickest at the free inner edge, more gradually blending with the muscles at the outer margin, with smooth or characteristically sculptured surfaces, the peculiarities of which may differ greatly in the various species. They are placed somewhat horizontally at each side of the buccal cavity, but working against each other; they are probably, however, functionally feeble and serve more especially as points of attachment to the various muscles actuating the radula and buccal bulb generally.

The Tetragnatha (τετρα-, four; γνάθος, the jaw) or quadrimaxillate species are exemplified by *Cyclostoma elegans*, in which the paired lateral jaws are placed on each side of the radula, each lateral pair being composed of a small and somewhat cuneiform posterior segment more or less intimately adherent by its contiguous margin to the anterior and larger one, which is of an irregularly oval form, with sinuate inner margin and a somewhat hexagonally papillate surface, the papillæ being arranged in somewhat regular series, mainly tending to converge towards the sinus on the inner margin, to which side this peculiar sculpture is more particularly restricted.

Fig. 503. — Pleurognathous Quadrimaxillate mandibles of *Cyclostoma elegans* (Müll.), from Box Hill, Surrey, collected by Mr. W. Whitwell, × 12, showing the peculiar sinuation of the inner margins and the irregularly hexagonal sculpture of the larger segments (photographed by Mr. T. W. Thornton from a careful preparation by Mr. J. W. Neville).

The Dignatha (δύο, two: γνάθος, jaw) are by far the most numerous Streptoneurous group, embracing all the bimaxillate species, of which *Bythinia tentaculata* may be taken as typical. Like *Cyclostoma*, the *Bythiniæ* are often stated to be entirely destitute of jaws, but they really possess two, one at each side of the buccal cavity, both of which are of a somewhat mytiliform shape, almost perfectly transparent and totally without noticeable surface sculpture. The smaller segments of the quadrimaxillate jaws have in the Dignatha become lost or perhaps fused with the larger anterior segments, which are now alone present.

Fig. 504.—Pleurognathous bimaxillate mandibles of *Bythinia tentaculata* (L.), × 20, from canal, near Nottingham, collected by Mr. A. G. Stubbs, showing the peculiar mytiliform shape and smooth unsculptured surface (photographed by Mr. T. W. Thornton from a careful preparation by Mr. J. W. Neville).

Certain extra-British pulmonate species are, according to Lang, dignathous, although not pleurognathous, the jaws being placed on the roof and floor of the entrance to the buccal cavity.

In *Valvata*, however, which in many features is of very primitive organization, there is a vestigial indication of an upper jaw, and it thus links together the tri-maxillate hermaphrodite forms with the bi-maxillate dioecious ones, forming another curious feature in its somewhat anomalous organization.

The Trignatha (τρί-, three: γνάθος, jaw) or trimaxillate species are, in this country, practically confined to the *Limnæidæ*, and are characterized by the possession of a well-developed transverse upper jaw, with sometimes a prominence upon the free edge and a pair of lateral jaws which are generally much smaller and slighter, and sometimes almost vestigial, but in some of the species of *Planorbis* and *Ancylus* the dorsal and lateral limbs have apparently become more or less fused together and thus form a single horse-shoe shaped buccal plate.

Fig. 505. — Trignathous dorso-pleural mandibles from *Limnæa peregra* (Müll.), × 20, Christchurch, Hants.

In *Limnæa peregra*, which may be regarded as a typical representative of this group, the well-developed, convex and somewhat lenticular upper or dorsal jaw is of a reddish horn-colour, but blackish along the free cutting edge, which, although exhibiting an

irregular contour in immature animals, in the adults presents a distinct median notch, with usually a broad flat projection at each side and a more prominent angle towards the outer margins, the projecting angles indicating the marginal terminations of four slight and indefinite rib-like thickenings which can in some lights be occasionally detected. The acute ends of the dorsal jaw are firmly attached to the pointed extremities of the almost linearly crescentic lateral jaws, which are placed at right angles to the upper jaw and have their concavity outwardly directed.

In action the dorsal and lateral jaws do not move simultaneously, but the upper jaw is first brought down and the side jaws close up laterally.

The Monognatha (μόνος, single : γνάθος, jaw), or mollusks with a single mandible, usually possess a more or less semilunar or crescentic jaw of a hard and chitinous nature, placed dorsally at the entrance to the oral cavity and varying in consistency from a very thick to quite a delicate substance, and from a deep opaque brown to a translucent amber, the colour being always deepest along the free cutting edge; but in some groups, as *Pupa*, the entire jaw has the appearance and colour of cartilage.

Fig. 506.—Oxygnathous jaw of *Limax maximus* L., in process of development, showing its bilateral origin, magnified (after Wiegmann).

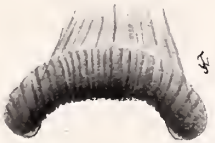


Fig. 507.—Mandible of *Helix pulchella* Müll., × 40, Seamer, near Scarborough, collected by Mr. J. A. Hargreaves, showing the posterior palatal extension. (Photographed by Mr. T. W. Thornton from a preparation by Mr. J. W. Neville.)

The Monognathous jaw really originates, according to Wiegmann, as two separate lateral parts, which afterwards unite in the median line, thus furnishing further corroborative evidence of the derivation of the monognathous jaw from a more ancient type, composed of a greater number of parts.

From the posterior lower margin of the jaw there arises a partially chitinous plate or membrane, which extends taperingly backwards upon the roof of the buccal cavity, gradually blending with it, and doubtless strengthening the jaw and its cutting edge ; this feature attains its maximum development in the distinctly defined palatal plate of the Elasmognatha. Mr. W. G. Binney however, as I think

erroneously, evidently regards the palatal plate of the Elasmognatha as not homologous with the mandibular palatal extension found in other monognathous groups.

In the monognathous species the mandible is opposed by the divided lower lip, which acts the part of a lower mandible in grasping the substance to be devoured and enabling the odontophore to rasp off particles of food, which are carried to the œsophagus by its action.

The Monognatha may be ranged under five chief groups, viz. :— Pycnognatha, Odontognatha, Leiognatha, Oxygnatha, and Elasmognatha, which are respectively characterized by the absence or presence of several more or less vertical thickenings or ribs, more especially upon the anterior surface of the jaw, by the development of a median projecting beak or by the possession of a large quadrangular accessory palatal plate.

The Pycnognatha (πυκνός, crowded ; γνάθος, jaw) often possess a somewhat convexly arcuate jaw, without the median beak or projection. It is especially characterized by the numerous fine and delicate vertical ribs, sometimes covering the whole anterior surface of the jaw, though occasionally only perceptible towards the cutting edge, which thus becomes finely crenulate. Amongst our monognathous Stylommatophora, this type of mandible is probably the first stage in the specialization of the primitive composite jaws which still characterizes our *Helix pygmæa* and other species, this modification arising from the fusion of the originally separated plates, the over-lapping lines of junction giving rise to the characteristic vertical striæ, although, as suggested by Pilsbry, this condition may also be reached through the odontognathous stage by the degeneration of the ribs. The *Bulimini* and some Helices are examples of this group.

Fig. 508.—A Striated or Pycnognathous mandible, × 40, *Helix pulchella* Müll., from Seamer, near Scarborough, collected by Mr. J. A. Hargreaves. (Photographed by Mr. T. W. Thornton from a preparation by Mr. J. W. Neville.)

The Odontognatha (ὀδούς, tooth : γνάθος, jaw) is well illustrated by the *Arionidæ* and many *Helicidæ* and embrace those species whose jaws bear, especially upon their anterior surface, more or less numerous and prominent parallel or slightly convergent ribs, which project beyond and denticulate the free margin, and sometimes the upper margin also. These ribs and their denticulations are usually more distinctly developed where their number is limited and less strongly marked when more numerously present,

but young shells have fewer and less prominent ribs and denticles than older specimens, the median ribs first appearing and development following on towards the extremities of the jaw, thus being analogous to the growth of the teeth in man, whose incisors or cutting teeth first appear, these being followed by the molars, etc., and lastly by the wisdom teeth. In addition to these well-marked ribs, there are numerous fine vertical striæ and also incremental striæ or lines of growth, which are parallel with the cutting edge.

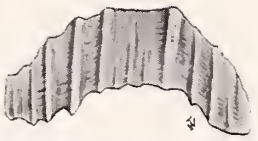


Fig. 509.—A Ribbed or Odontognathous mandible, *Helix pomatia* L., × 10, from Preston Candover, Hants., collected by the Rev. H. P. Fitzgerald.

Mr. Crowther has shown that the strength of the jaw and the number of the ribs may be modified by the environment, a soft, succulent herbage developing few ribs on a comparatively delicate jaw, while the same species living on coarser fare by dusty road-sides have a harder jaw with stronger and more numerous denticles, but the immature animals always possess a more delicate jaw, with fewer and slighter ribs, than their mature companions in the same locality.

The Leiognatha (λεῖος, smooth; γνάθος, jaw) typically possess a smooth mandible or jaw, from which all the striation has become obliterated and which show no trace of the median rostrum or beak, which is so striking a feature in the oxygnath jaw and may be viewed as the antithesis of the odontognatha; in Leiognatha the jaw has lost all trace of ribs or striæ and is apparently of homogeneous composition, while in the odontognatha the ribs and denticulations have assumed great prominence.

Fig. 510.—An Unstriated or Leiognathous mandible, *Pupa cylindracea* (Da Costa), × 40, Beverley, collected and prepared by Mr. J. D. Butterell.

The Oxygnatha (ὀξύς, sharp; γνάθος, jaw) are exemplified by the *Limacidæ* and *Vitrinidæ*, which possess a jaw strongly arcuate from front to back, but smooth on the surface, owing probably to the disappearance of the delicate riblets, characteristic of the pycnognatha; they are, however, more especially distinguished by being vertically carinate in the centre, the keel terminating in a median beak or projection on the cutting margin.

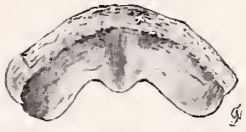


Fig. 511.—A Rostrate or Oxygnathous mandible, *Limax flavus* L., × 10, Christchurch, Hants.

The Elasmognatha (ἔλασμα, a metal plate; γνάθος, jaw) or Appendiculate jaw is a type whose great peculiarity consists in the development of a very large, somewhat square accessory palatal plate, which extends posteriorly backwards upon the roof of the mouth; it is of similar material and consistency and about two-thirds the width of the jaw itself, with which it exhibits continuity of structure. The upper portion of the jaw is imbedded in the tissues, and the free portion is characteristically horse-shoe shaped with a strong and pointed median projection.

Fig. 512. Fig 513.

Fig. 512 front view and Fig. 513 side view of the Appendiculate or Elasmognathous mandible of *Succinea putris* (L.), × 25, from Christchurch, Hants., showing the convexity of the jaw generally and the strongly developed accessory palatal plate.

The Elasmognath jaw is restricted in this country to the genus *Succinea*, although our species vary somewhat in the character of the jaw itself, *Succinea elegans* possessing a practically oxygnath jaw upon which the posteriorly projecting palatal appendage is developed, while *Succinea putris*, in addition to the well marked median beak or rostrum, which is the characteristic of the oxygnatha, also displays strong and distinct transverse radiate ridges, simulating those of the true odontognathous species.

The Odontophore (ὀδούς, tooth; φέρω, to bear), Radula, or lingual ribbon, is a tongue-like cartilaginous process projecting upon the floor of the buccal cavity, and forming a somewhat prehensile apparatus, with its free surface covered with an immense number of minute, backwardly directed teeth, arranged in regular longitudinal and transverse rows, and of strikingly different forms in the different genera and species, the whole resting upon the sub-radular membrane, which is continuous with the lining of the buccal cavity, and placed upon the two somewhat confluent odontophoral cartilages, which are closely united in the median line by fibrous and muscular tissue. The very general possession of this organ, in a very large section of the mollusca, has led to the term Glossophora, or tongue-bearing, being applied to the groups possessing it.

The Radula Sac, from which the radula is developed as a somewhat tubular outgrowth, is an epithelial invagination of variable length in the median line of the floor of the mouth or buccal cavity,

often posteriorly extended beyond the buccal bulb. It is filled with connective tissue and its distal ventral walls bear the Odontoblasts (ὀδούς, tooth ; βλαστός, a bud) or tooth-forming cells, a few cells with large nuclei and clear protoplasm, as in the Pulmonates, or a greater number of smaller cells, only distinguishable from ordinary epithelial cells by their greater length, but whose arrangement always coincides with that of the teeth they secrete ; these, however, after their formation by the odontoblasts, become hardened for use by a superficial deposit of "enamel" from epithelial cells above the radula, and are then of an amber colour, an appearance which is soon lost and the teeth blunted, broken and worn away when they come into active use ; this wearing away and loss of the anterior functional part of the radula is compensated for by the progressive growth from the radula sac of newly-formed teeth and their supporting membrane, exactly like a finger nail on its bed, in which the wearing away of the anterior free margin is compensated for by its own forward growth. According to Dr. Sterki, *Limax campestris*, which is closely allied to, if not actually identical with, our *Agriolimax lævis*, forms in this way not less than 800 transverse rows of teeth during its ordinary life-term, and this implies at least eight entire changes of denticles ; some Helices he affirms produce 2,000 or more transverse rows, indicating 16—18 total changes of teeth by the animal.

Fig. 514. — Epithelial cells from pharynx of *Helix pomatia* L., highly magnified (after Vogt and Yung).

Fig. 515.—Diagrammatic longitudinal section through the posterior end of the radula sac of a Pulmonate, showing the teeth and basal membrane in process of formation (after Rössler).

b.m. basal membrane of the radula ; *c.* formative cells of the basal membrane ; *od.* odontoblasts or formative cells of the radular teeth ; *t.* radular teeth.

The Development of the radular teeth in the embryo begins in the form of mere chitinous nodules, which, in the succeeding transverse rows, acquire many long and sharply pointed cusps or processes before eventually attaining the adult or permanent form ; this transitory phase in their development has been termed the Echinate (ἐχῖνος, a hedgehog) stage. At first there are also fewer longitudinal rows of teeth than are afterwards present, the additional rows being added at the outer margins and not interpolated between the rows

already present; these also originate in the nodular form, pass through the echinate stage and in the succeeding transverse rows gradually acquire the characters of true marginals; the laterals also, in the same way, increase somewhat correspondingly in number by the gradual change of what were the marginals of the embryonal mollusks into the laterals of more mature animals, the character of the teeth in the longitudinal series and their relative position on the membrane becoming modified thereby. These changes are peculiar to the embryonal stage and due to modifications of the odontoblasts, as the same group of cells forms all the teeth in the same longitudinal row, this fact elucidating the cause of the unvarying recurrence of deficient, deformed or abnormal teeth the whole length of the radula, which has been so often observed.

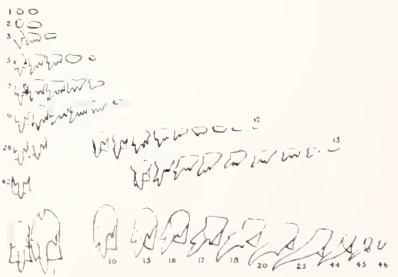


FIG. 516. — Radula of an embryo of *Limax campestris* showing the nodular character of the teeth on first development and the changes undergone in passing through the Echinate intermediate stage before attaining the adult form, highly magnified (after Sterki).

The lowermost series is that of an adult.

The perpendicular row of numerals indicates the number of transverse rows that have existed on the radula, reckoning from their first development.

The horizontal numerals give the position of the individual teeth in the transverse rows reckoning from the central tooth.

The MUSCULAR DEVELOPMENT of the buccal mass is exceedingly complicated and varies in arrangement in the different groups, as many as twenty distinct extrinsic and intrinsic muscles having been distinguished as concerned in the efficient use of the radula alone,

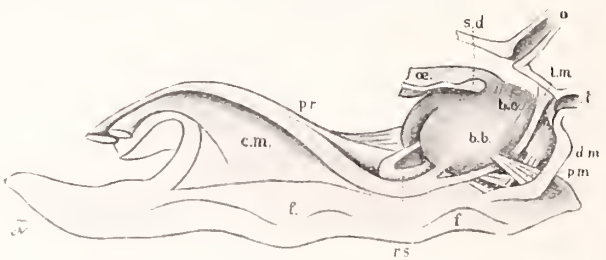


FIG. 517.–Dissection showing the Extrinsic buccal muscles of *Helix aspersa* Müll. (after Howes).
b.b. buccal bulb; *b.c.* constrictor muscles of buccal bulb; *c.m.* columellar muscle; *d.m.* depressor muscles; *f.* foot; *l.m.* levator muscles; *o.* ommatophore; *œ.* œsophagus; *p.m.* buccal protractors; *p.r.* pharyngeal retractor; *r.s.* radular sac; *s.d.* salivary ducts; *t.* anterior tentacle.

their alternating contractions and relaxations causing the radula to travel backwards and forwards and thus rasp against any object to which it may be applied, the presence in their substance of

hæmoglobin testifying to the increased respiratory activity necessitated by their vigorous movements.

The Extrinsic muscles pass from the odontophore, chiefly to the outer walls of the prosoma, and actuate the entire organ; they are known as Retractors, Protractors, Levators, or Depressors, according to the function they perform. The Protractors pass forwards and downwards from the buccal bulb to the cephalic integument and protrude the radula; the Levators are above the Protractors and affixed to the cephalic wall near the anterior tentacles; the Depressors underlie the Protractors and pass obliquely backwards, and, with the Levators, assist to determine the special licking motion of the protruded radula, which is then bent over the supporting cartilage in front of the oral aperture: the Retractor is a powerful muscle or series of muscles with a bifid or multifid attachment to the buccal bulb, and distally affixed to the columella of the shell or to the integument itself in the nude species.

FIG. 518.—Muzzle retractor of *Cyclostoma elegans* (Müll.), × 3 (after Simroth).

r.m. retractor muscles; *l.m.* muscles, whose action gives the licking motion to the odontophore.

The Intrinsic muscles also consist chiefly of Retractors and Protractors which arise from the walls of the buccal bulb and are affixed to the posterior and anterior parts respectively of the radula, chiefly controlling its lesser movements and also spreading out the radula during its protrusion, thereby divaricating and erecting the individual teeth for effective use; the sides again converging during retraction and forming a somewhat prehensile apparatus. All species, however, do not use their odontophores in precisely the same way, as, according to Dr. Sterki, *Planorbes* move the radula from behind, forward; *Physa* the sides towards the centre, while in *Limnæa* the radular motion is a combination of the two methods; the various

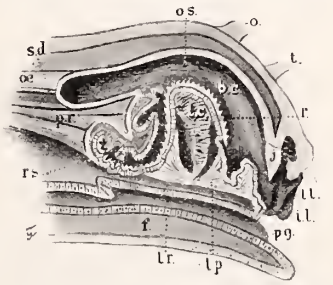


FIG. 519. — Median longitudinal section through the prosoma of an Euthyneure (modified after Howes), × 3, showing the disposition of the Intrinsic radular muscles, and incidentally the arrangement of the jaw and the organs of the prosoma generally.

b.c. buccal cavity; *f.* foot; *i.l.* inner lip; *j.* jaw or mandible; *l.c.* lingual cartilage; *l.l.* lower lip; *l.p.* lingual protractors; *l.r.* lingual retractors; *o.* ommatophore; *œ.* œsophagus; *o.s.* orifice of left salivary gland; *p.g.* pedal gland; *p.r.* pharyngeal retractors; *r.* radula; *r.s.* radula sac; *s.d.* right salivary duct; *t.* anterior tentacle.

modes of using the odontophore when feeding are also graphically shown when snails have fed upon the paste and whiting mixture so frequently applied as a summer shading to greenhouse roofs; the serpentine or meandering series of more or less pyriform figures impressed upon the compound by the licking action of the tongue are seen to differ in their arrangement according to the species, showing that each kind of snail when feeding moves its head from side to side in a more or less characteristic manner as the animal advances, but generally speaking, the method of using the odontophore resembles that of the tongue of a cat when licking, this action rasping particles from the food to which the radula is applied.

FIG. 520.—Track of *Helix aspersa* formed by feeding on the paste and lime shading upon a greenhouse roof, Christchurch, Hants, June, 1883.

The RADULAR or BASAL MEMBRANE, to which the teeth are attached and which together with the teeth form the radula, is also formed within the radular sac, by the transverse range of secretory cells anterior to the odontoblasts splitting at the ends into fibres, which are placed side by side, the whole being supported upon the paired lingual cartilages, wherein are numerous branched cartilage cells imbedded within a clear matrix, and to which some of the muscles actuating the radula may be attached. At the base of the cartilages and anterior to the free end of the radula, there is usually a sac-like depression in the floor of the buccal cavity, the significance of which is not as yet understood.

The Surface of the Radular Membrane may be divided longitudinally into five areas, grouped as the Central, the Admedian and the Marginal, one or more of which may be deficient in special groups or genera.

The Central or Rachidian area is the narrow longitudinal mid-region or Rachis, and bears the median teeth; the Admedian areas or Pleuræ are paired and placed at each side of, and adjoining the median one; they bear the asymmetrical lateral teeth, while the two Marginal areas are occupied by the marginal teeth or uncini, the particular features of each type of tooth being correlated with its position upon the radular membrane.

The Radular Teeth or denticles, according to their position and character, may also be classified as Central, Admedian or Lateral, and Marginal, and are all reflected posteriorly, the reflected points or cusps being known as Mesocones, Ectocones or Endocones, according to the relative position they occupy on the individual teeth.

The Central teeth, which occupy the rachis or longitudinal mid-line of the radula, are symmetrically formed, but do not originate by the coalescence of two adjoining laterals, except perhaps among the *Limnæidæ*, in which the central teeth may, as in *Planorbis*, show no central cusp, but two equally developed lateral cusps. The convex anterior margin of each tooth often overlaps the base of the preceding tooth, and is usually trifidly reflected posteriorly, the median reflection or cusp being known as the Mesocone and the smaller side cusps as the Ectocones.

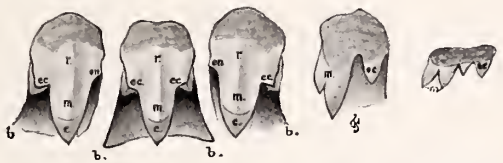


Fig. 522. Fig. 521. Fig. 523. Fig. 524. Fig. 525.

Fig. 521.—Central or Median Tooth of *Helix aspersa* Müll., highly magnified.

b. basal plate ; *r.* reflected portion ; *m.* mesocone or middle cusp, with *c.* cusp or cutting point ; *ec.* ectocone or outer cusp with cutting point.

Figs. 522, 523.—Admedian or lateral teeth of *Helix aspersa* Müll., from right and left sides of and adjacent to the median row.

b. basal plate ; *r.* reflected portion ; *m.* mesocone or middle cusp, with *c.* its cusp or cutting point ; *en.* endocone or inner cusp ; *ec.* ectocone or outer cusp.

Fig. 524.—Intermediate or Transition tooth of *Helix aspersa* Müll.

m. mesocone, showing endoconic bifurcation ; *ec.* ectocone or outer cusp.

Fig. 525.—Marginal tooth or Uncinus of *Helix aspersa* Müll.

m. bifid mesocone ; *ec.* bifid ectocone.

The Admedian or Lateral teeth occupy the Pleuræ or longitudinal areas, adjoining the central one, and are usually asymmetrical modifications of the median teeth, becoming more and more primitive, or unlike the symmetrical central teeth the further they recede from them. The anterior margin is strongly reflected posteriorly, the term Mesocone being retained for the reflection, representing the middle projection of the rachidian series ; the term Ectocone designating the cusp nearest the outer margin, while the cusp on the inner side of the tooth, nearest the centre of the radula, is called the Endocone.

The Marginal teeth or Uncini occupy the longitudinal outer areas of the radular membrane, and in many species show a wider base and more numerous denticulations ; they also tend to approach

the median line at a more acute angle than the lateral teeth usually do, and viewed by the light of their development, are the most primitive form of tooth existent on the odontophore.

The change in character from the symmetrical median tooth to the asymmetrical laterals and marginals is usually decisive and may be marked, amongst other things by the partial or entire loss of the endocone or inner cusp and a corresponding enlargement of the mesocone or middle cusp, which with the ectocone or outer cusp may become deeply cleft, this divergence of character becoming more and more marked as the outer fringe of the radula is approached, and being also more or less closely correlated with the direction or curvature of the transverse rows, which is greatly varied in the

FIG. 526.

FIG. 527.

FIG. 528.

FIG. 529.

Diagrammatic figures showing the varied directions of the transverse rows of teeth in different species.

FIG. 526.—*Testacella haliotidea* Drap.
FIG. 527.—*Velletia lacustris* (L.).
FIG. 528.—*Helix lapicida* L.
FIG. 529.—*Physa fontinalis* (L.).

different species, an abrupt change in their direction being always accompanied by an equally marked change in the character of the teeth, while if the rows are straight or the change of direction very gradual, this change is correspondingly slow, and between the well marked laterals and typical marginals several transitional teeth may be interposed.

A NOTATION or FORMULA has been devised to express, by means of signs and numbers, the general arrangement and some of the more salient characters of the radula of many of our species. The possibility of doing this is simplified by the transverse rows of teeth being bilaterally alike, while the longitudinal rows are each straight and contain similar teeth along their whole length.

The writing of the formula is accomplished by placing a numeral to represent the central tooth, the particular numeral used according with the number of central teeth present in a transverse row; the same course is pursued with the laterals and marginals when these are homogeneous in shape and character, the numerals representing which, separated by the sign +, are placed at each side of the central figure in similar positions to those actually occupied by the teeth

themselves; thus the formula $20+4+1+4+20$, would indicate that in each transverse row there was one central tooth flanked by four lateral and twenty marginal teeth, each series of a practically homogeneous character. Sometimes the marginals are so minute and compact or so numerically variable that it is difficult or impossible to state their exact number; in such cases the sign of infinity (∞) may appropriately be used to indicate them. When, however, the teeth composing a series are markedly heterogeneous in form and general character, the numerals representing them may be used individually or in suitable combinations, so that their dissimilarity may be emphasized, thus $\infty+1.1.1.1.+1+1.1.1.1.+\infty$ would signify that there was one central tooth, with four dissimilar laterals, and an indefinite number of homogeneous marginals at each side.

The number of transverse rows should also be added to the formula, preceded by the sign $\times$, which will often enable the total number of teeth on the radula to be readily ascertained if desired, as although their number is approximately constant in full-grown individuals of the same species, it varies very considerably in different groups and even in different species, and is not at all dependent on the size of the animal, for *Hyalinia lucida* has only about 945 denticles, whereas *Helix obvoluta*, a species of about the same dimensions, has 15,300.

Increased precision in notation may be attained by the use of larger or smaller figures to indicate the relative sizes of the teeth and also by placing beneath the numeral representing the number of teeth in each group, a second series to denote the number of reflections or cusps upon the individual teeth; if these consist of a variable number of minute and numerous pectinations, they may be indicated by the sign of infinity ∞, as already suggested for the representation of marginal teeth when numerously present; where, however, the number of teeth or pectinations do not exceed 20, and the amount of variation is not accurately known, it will be more satisfactory to give the ascertained number as near as may be with the marks of increase or decrease as most appropriate, thus $14<$ would convey the information that 14 or more teeth or pectinations were present; <14 that the variation was towards a lesser number, while $<14<$ would indicate that the quantity present ranged above and below the number indicated, thus:

$$\underset{1-2}{\overset{\geq 0+1}{}}+\tfrac{2}{3}+\tfrac{1}{3}+\tfrac{2}{3}+\underset{2-1}{\overset{1+0\leq}{}}\times 38=950,$$

the full dental formula for *Hyalinia alliaria*, shows that species, in the particular preparation examined, to possess 950 teeth, contained

in 38 transverse rows, each with a trifidly reflected median tooth, flanked on either side by two lateral teeth with three cusps, and by ten or more aculeate marginal teeth, the innermost having two cutting points and being transitional in character.

FIG. 530. — Transverse row of teeth from the odontophore of *Hyalinia alliaria* (Miller highly magnified, from a micro-photograph by Mr. W. Moss.

The CLASSIFICATION of the odontophores of our native species is a task of considerable difficulty, but their study at once suggests the desirability of separately considering and grouping the Streptoneurous and Euthyneurous forms.

The STREPTONEURA have long been known to possess such very persistent and characteristically varied types of teeth that their peculiarities have, by almost universal consent, been utilized as a basis for forming natural groupings of this section of the mollusca. Our Streptoneurous species may all be placed under the two well-known groups, Rhipidoglossa and Tænioglossa.

The RHIPIDOGLOSSA (ῥιπίς, fan; γλῶσσα, tongue) are especially characterized by the extraordinary number and marked uniformity of the uncini or marginal teeth, which are usually very compactly arranged in a somewhat curvilinear or fan-like manner, diminishing gradually in size as they approach the outer margins of the radula.

FIG. 531.—Transverse row of teeth from the odontophore of *Neritina fluviatilis* (L.), highly magnified, River Nene, Northampton, collected by Mr. L. E. Adams, B.A., and prepared by Mr. J. W. Neville.

In *Neritina fluviatilis*, our only representative of this group, the central teeth are obscurely trifid, the laterals of very dissimilar size and shape, with the first and the outermost of the series exceptionally

large and broad; the former may be known as the Major lateral, to mark its superior size, while the latter is distinguished as the Capituliform tooth, on account of its fancied resemblance to the capital of a column; the marginals are very numerous and compact with two or more cusps. The formula may be expressed as

$$\frac{x}{>2} + \frac{1+1+1+1}{x\ \ 3} + \frac{1}{3} + \frac{1+1+1+1}{3\ \ x} + \frac{x}{2<} \times 68.$$

The affinity of the terrestrial air-breathing genera, *Helicina* and *Proserpina*, to our branchiate *Neritina fluviatilis* is demonstrated by the similarity in character of their dentition.

The TÆNIOGLOSSA (*ταινία*, ribbon; *γλῶσσα*, tongue) to which practically all our Streptoneurous species belong, are chiefly remarkable for the extraordinary length and narrowness of the radula. They are usually characterized by bearing seven longitudinal rows of teeth, composed of a central tooth, with one or sometimes two somewhat

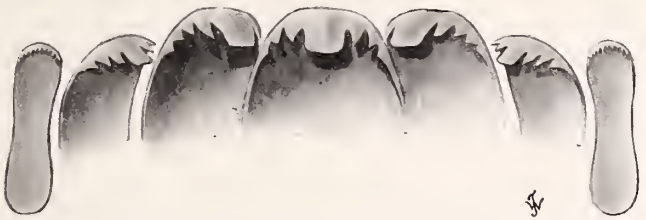


FIG. 532. — Transverse row of teeth from the odontophore of *Vivipara vivipara* (L.), highly magnified, Northampton, collected by Mr. L. E. Adams, B.A., and prepared by Mr. J. W. Neville.

ample admedian or lateral ones, and one or more, but usually two, more slender marginals at each side, all closely serrate or dentate at the upper or cutting edge and the outer series often outwardly directed.

This type of dentition is shown by *Vivipara vivipara*, whose chief peculiarities may be expressed by the formula

$$\frac{1}{10-12} + \frac{2}{7-9} + \frac{1}{7} + \frac{2}{7-9} + \frac{1}{10-12} \times 90 = 630,$$

signifying that there are 630 teeth upon the membrane arranged in 90 transverse rows, each containing a central tooth, flanked on either side by two lateral teeth and a single marginal, all strongly pectinated upon their cutting edges, the chief feature of which is the large quadrangular central cusp, present upon all the teeth except the marginals or uncini.

A similar general arrangement is found amongst the Nucleobranchs, in which, however, the lateral teeth are more strictly aculeate, corresponding to their more carnivorous habits of life.

The EUTHYNEURA or pulmonate species, the most highly specialized of the Gastropoda, were all formerly relegated to the Ctenoglossa, a group to which *Clio*, *Actæon*, *Helicina*, *Limnæa*, *Helix* and other terrestrial, fluviatile and marine genera were also referred.

After careful study and examination of many types, I have tentatively placed our Euthyneurous species in two chief divisions, Stenodontophora and Eurydontophora, based upon the more or less broad and quadrate or narrow and sole-shaped form of the basal plates by which the teeth are attached to the lingual membrane.

The STENODONTOPHORA (στενός, narrow ; ὀδούς, tooth ; φέρω, to bear) are those species or genera with teeth of an aculeate character affixed to the radular membrane by a narrow and somewhat sole-shaped base of attachment, from the whole surface of which there arises a strongly recurved spine-like tooth.

FIG. 533. — Typical Aculeate or Acanthoglossate tooth showing the sole-shaped base of attachment, highly magnified.

The surface of the radula usually presents a median and two marginal areas, and typically the teeth are uniform in character in each series, the median row, when present, being sometimes formed by trifidly reflected teeth, and the marginals varying only in the size they attain, the largest and most powerful being placed near the outer margins, corresponding to the prominences of the lingual cartilage and the greater functional importance thus conferred by that position in the seizure of prey, while those nearest the median line and the extreme marginals are the smallest, a gradual increase of size taking place from the median line and a much more rapid and decisive enlargement from the outer marginal series.

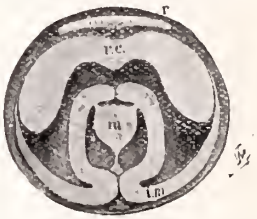


FIG. 534.—Section across the head of *Testacella haliotidea* Drap., showing the form of the lingual cartilage and the disposition of the radula, etc. (after Lacaze-Duthiers).

m. matrix ; *i.m.* intrinsic muscles; *r.c.* radular cartilage with superimposed radula.

It is the type of radular teeth for carnivorous mollusks and is characterized by comparatively limited series of long, narrow, loosely ranked spinous teeth, which approach the median line from the lateral margins at a posteriorly directed acute angle, as in *Testacella* ; but in *Physa fontinalis* the angle formed, although equally acute, points in the opposite direction.

The Stenodontophorous species, according to the character of the apices of the teeth or the modification they have undergone, may be divided into three chief groups, viz. : Acanthoglossa, Beloglossa and Echinoglossa.

The ACANTHOGLOSSA (ἄκανθα, a prickle ; γλῶσσα, tongue) possess spine-like or sickle-shaped teeth (as fig. 533), a form which would seem more especially to characterize the carnivorous genera, but no species under our especial survey possesses a radula exclusively formed of this type of tooth, although *Rhytida* and other tropical genera show characteristic examples ; this group is, however, enumerated here as some of our genera possess Acanthoglossate teeth in conjunction with those of the Pycnoglossate type, and in such cases the Acanthic teeth always form the marginal series and generally tend to approach the median line at a more acute angle than the quadrate teeth usually do.

The teeth may be simply thorn-like or, by cleavage of the apex, form bispinose or trispinose teeth, the accentuation of this feature becoming more and more marked as the margin of the radula is approached.

The *Proctonotidæ* amongst the Opisthobranchs and *Rhytidæ* among the Pulmonates show characteristic examples of this type, almost identical in form and arrangement.

The BELOGLOSSA (βέλος, an arrow; γλῶσσα, tongue) or species with barbed teeth are confined in this country to the predatory genus

FIG. 535.—Transverse row of the teeth from the odontophore of *Testacella haliotidea* Drap., highly magnified, from Oxford, collected by Prof. Poulton and prepared by Mr. J. W. Neville.

Testacella, and would appear to be a special modification of the Acanthoglossate type, adapted to more securely retaining their hold upon the earthworms upon which the *Testacellæ* chiefly prey.

The odontophore of *Testacella haliotidea* may be formulated as

$$>\frac{1\,8}{1} + \frac{0}{0} + \frac{0}{0} + \frac{0}{0} + \frac{1\,8}{1}< \times 38 = 1{,}368,$$

showing that there are 1,368 teeth arranged in 38 transverse rows, all of which are deficient of the middle and lateral series, but possess 18 marginal teeth at each side, all of which are strongly barbed on one side of the apex like a fish-hook and may also be furnished with a sharp blade-like cutting edge on the convex side of the apex. The base of attachment acquires knobbed extremities, owing to the enlargement of each end, for firmer attachment to the radular membrane.

Typically the Beloglossate radulæ are deficient of a median row of teeth, although a minute mid-tooth may occasionally be met with in some part of the membrane.

The Echinoglossa (ἐχῖνος, a hedgehog; γλῶσσα, tongue) may be an aberrant form of the Acanthoglossate teeth, with more numerous spinous terminations and a more pronounced curve of the reflected portion or more probably it may have arisen from a different stock, as the radical difference in the mode of convergence of the lateral transverse rows would seem to point to a different derivation.

Fig. 536.—Median portion of a transverse row of the teeth of *Physa fontinalis* (L.) highly magnified, from Cambridge, collected and prepared by Rev. Prof. Gwatkin, M.A.

The Echinoglossa are not only remarkable for the large accessory oval plate or knob attached to and projecting anteriorly beyond the teeth, but also for the acute convergence of the transverse rows from the lateral margins towards the anterior portion of the membrane, instead of towards the posterior end as in mollusks generally.

The individual teeth are very closely and compactly arranged, except near the median line, where the smaller size of the teeth leaves a perceptible space between the transverse rows; the mid-tooth shows long and prominent lateral margins, which in *Physa fontinalis* are partially overwrapped by or fused with the adjacent teeth. The marginals are very numerous and practically uniform throughout, varying only in the number of cutting points they display.

This type of tooth is possessed by *Physa fontinalis*, and its characters may be broadly expressed by the formula

$$\frac{>1\,7\,4}{>8} + \frac{1}{x\ 1\ x} + \frac{1\,7\,4<}{8<} \times 57 = 19{,}893.$$

The genus *Chilina*, a primitive group of fluviatile snails inhabiting South America, has teeth of the same general character, bearing a similar knobbed enlargement of the anterior end of the base of attachment and the transverse rows of teeth having the same anteriorly directed arrangement.

The EURYDONTOPHORA (εὐρύς, broad; ὀδούς, tooth; φέρω, to bear) are those species with teeth characterized by a somewhat square base of attachment to the radular membrane, and distinguished from the Aculeate type of teeth by their gradual diminution in size, in proportion as they recede from the centre of the membrane, their greatest development being near the centre—perhaps in correlation with the median longitudinal ridge upon the lingual cartilage, which probably endows the teeth thereon with increased functional importance, and leads to their acquiring greater strength than those less favourably placed for the efficient exercise of their powers.

FIG. 537. — Transverse section through the buccal bulb of *Agriolimax agrestis* (L.), ×30, showing the form of disposition of the radula and radular cartilages (after Hanitsch).

b.c. buccal cavity; *m.* ventral muscles of buccal bulb; *r.c.* radular cartilages with superimposed radula; *s.d.* salivary ducts.

The teeth are usually divisible into three series, distributed upon a central, two lateral, and two marginal areas; the lateral and marginal areas, however, often blend so insensibly together that no distinct line of separation can be made out between them; this doubtful space bears teeth of a similar undecided character, as they partake of the characters of both series and are known as transitional teeth.

FIG. 538.

FIG. 539.

FIG. 538.—Typical Quadrate or Eurydontate tooth as seen from above, highly magnified.

FIG. 539.—Side view showing the reflection and cutting points, highly magnified.

The Eurydontophora have usually numerous transverse rows of closely-set cuspidate teeth, a form especially adapted for the reduction of vegetable food, and, according to the character of the individual teeth, may be tentatively arranged in four groups, viz., Pycnoglossa, Zeugoglossa, Myriaglossa and Dichoglossa.

The Pycnoglossa (πυκνός, crowded ; γλῶσσα, tongue) may be considered as the typical dentition of the Pulmonates generally and of the Helices in particular. It is characterized by the enormous number and close arrangement of the individual teeth, which resemble mosaic work in their compact methodical arrangement. The mid-tooth is usually trifidly reflected with the mesocone much the longest, while the laterals and marginals are more or less asymmetrical modifications of the type of the central tooth, each tooth becoming more numerously denticulate and with wider base as the margin is approached. The transverse rows are usually gently curved, approaching the median line at almost right angles. This gradual change in direction gives rise to intermediate or transitional teeth, connecting imperceptibly the

Fig. 540.—Representative teeth of half a transverse row of teeth o *Helix aspersa* Müll., highly magnified, collected by Dr. Scharff near Dublin.

The numerals appended to the figures of the teeth indicate their position in the transverse row.

lateral and marginal series. *Helix aspersa* is a typical example of this group, and its peculiarities can be expressed by the formula :

$$\geq\frac{1}{4}\frac{3+1}{3}\frac{0}{}+\frac{2}{2}\frac{0}{}+\frac{1}{3}+\frac{2}{2}\frac{0}{}+\frac{1}{3}\frac{0+1}{4}\frac{3}{}\leq\times 145=12{,}615,$$

showing that species to possess 12,615 teeth, contained in 145 transverse rows, each containing a central tooth, bearing 3 cusps, 20 laterals at each side with 2 cusps, and 33 marginals and transitional teeth, with 3—4 cusps each.

The Zeugoglossa (ζεῦγος, paired; γλῶσσα, tongue), of which *Planorbis corneus* may be taken as an example, are distinguished by the paired or bifid cusps to the teeth composing the median longi-

Fig. 541.—Representative teeth from a transverse row of the odontophore of *Planorbis corneus* (L.), highly magnified, collected at Northampton by Mr. L. E. Adams, B.A., prepared by Mr. J. W. Neville.

The numerals appended to the figures of the teeth indicate their position in the transverse row.

tudinal row ; the laterals being also bicuspidate and the marginals exhibiting the comb-like teeth of the Acanthoglossate type. The formula of *Planorbis corneus* may be written as :

$$\frac{2}{2}\frac{5}{-5}+\frac{8}{2}+\frac{1}{2}+\frac{8}{2}+\frac{2}{2}\frac{5}{-5}\times 200=13{,}400.$$

This peculiar dentition is in this country restricted to the *Planorbes*, but has been shown to be also possessed by their possible progenitors, the so-called *Physæ* of Australia, the representatives of which, although now restricted to the Southern Hemisphere, had probably in former times a much more extended range.

The MYRIAGLOSSA (*μυρίον*, numberless; *γλῶσσα*, tongue) have more simply shaped and uniform teeth than many of the other Eurydontophorous groups, and are characterized by the possession of a well-defined, though slender, mid-tooth, with a trifid reflection flanked by

FIG. 342.—Transverse row of teeth from the odontophore of *Helix pygmæa* Drap. (highly magnified), Cambridge, prepared by Prof. Gwatkin.

numerous closely set bicuspidate and obscurely tricuspidate teeth of a practically uniform and usually simple hooked character; the formula for *Helix pygmæa*, a representative of this group, may be expressed as :

$$\tfrac{4}{3}+\tfrac{1\,4}{2}+\tfrac{1}{3}+\tfrac{1\,4}{2}+\tfrac{4}{3}\times 48=1{,}776.$$

The DICHOGLOSSA (*δις χῶς*, double; *γλῶσσα*, tongue) are represented by the genera *Hyalinia*, *Limax*, etc., and are distinguished by possessing tricuspid median teeth, with variously cusped quadrate teeth on the central and pleural areas of the radula, the marginal series being formed by teeth of the Acanthoglossate or Echinoglossate type.

FIG. 343.—Transverse row of teeth from the odontophore of *Hyalinia nitidula* (Drap.), highly magnified, prepared by Mr. J. W. Neville.

The numerals appended to the figures of the teeth indicate their position in the transverse row.

Hyalinia nitidula may be taken as typical for this section, and the peculiarities exhibited by its odontophore may be formulated as

$$\tfrac{3\,0+1}{1\quad 2}+\tfrac{4}{2}+\tfrac{1}{3}+\tfrac{4}{2}+\tfrac{1+3\,0}{2\quad 1}\times 35=2{,}485.$$

This group may be looked upon as a link between the Aculeate and Quadrate teeth, as it combines both forms on the same membrane, and would thus seem to markedly indicate the omnivorous character of the species or groups possessing it. In this group certain genera will fall which further investigation may probably demonstrate to be more suitably classified under other heads.

The Preparation of the buccal armature is of such importance, not merely on account of the intrinsic interest of the organs themselves, but because their study sheds so much light upon other aspects of the science, that a brief account of the methods adopted for this purpose by Prof. Gwatkin, Mr. W. Moss, Mr. J. W. Neville and other prominent microscopists will be useful.

The mollusk is killed by immersion in boiling water and, if a species of moderate size, extracted from its shell, and the head carefully opened from above, when the buccal bulb containing the jaw and odontophore will be disclosed; if, however, the species be too small for convenient dissection in this way, the shell with the contained animal may be crushed between two glass slips.

The buccal bulb of the larger species or the crushed mass of the more minute ones are placed in a watch-glass or test tube containing a solution of Caustic Potash, and allowed to remain therein for a day or two to dissolve the muscular investment.

When greater expedition is desirable, the buccal bulb of the larger animals may be boiled in the potash solution in a test tube or watch-glass and the minute species upon the slide upon which they have been crushed, taking care in each case that the solution is not too strong.

When the desired organs are freed from extraneous matter, wash well in clean water and if necessary place in a weaker potash solution for a few hours; then give a final thorough washing, using, if thought advisable, a very fine camel's-hair brush to assist the cleansing process, more especially at the hinder end of the radula, but to secure the perfect removal of the potash, the radula may again be placed in pure water for some hours.

When thoroughly clean, the jaw and odontophore are transferred to and immersed in a small drop of glycerine with which the preparation will be thoroughly permeated in about half-an-hour, when they may be finally transferred to a clean slip, upon which a droplet of glycerine has been placed, and the jaw and odontophore arranged in the desired positions under the microscope. If the odontophore does not spread out flat this may be due to a constricting upper membrane, which, with a lower non-constricting one, needs careful removal. If the radula is unavoidably somewhat torn in the process, it will be no disadvantage, as it will enable the teeth to be examined in various aspects, and in fact it is desirable to purposely make a tear quite across the odontophore to achieve this result.

When satisfactorily arranged, breathe upon a clean cover-glass and place it upon the object without enclosing air-bubbles, and then, while carefully avoiding moving the glass cover, wipe off the superfluous glycerine with a soft rag, and with a fine brush dipped in quick-drying gold size run a connecting line round the glass cover and slide and lay aside for a day or two to dry, before finishing off with cement.

If Glycerine Jelly be preferred as the mounting medium, the bottle containing the jelly should be placed in a cup of hot water until liquefied, and when the radula and jaw are satisfactorily arranged on the slide, place a cover-glass over them, and secure it by a clip, before running the now fluid jelly beneath the cover, under which it will quickly penetrate by capillary attraction; when thoroughly permeated, boil for a moment to get rid of vacuoles or vapour bubbles, and place the slide aside in a cool place for two or three weeks; the superfluous jelly can then be removed and the mount completed with a ring of brown cement and a finishing coat of gold size. The objection to the use of glycerine is its hygroscopic nature, and in some districts the injurious effects resulting from this quality can scarcely be securely guarded against by the most careful ringing.

Canada Balsam is also used as a mounting medium when it is intended to stain the radula or where it is desired to use the polariscope in the examination of the preparations, and though the Balsam, in course of time, renders the teeth very transparent, that is no real obstacle to the successful use of the polarizing apparatus.

Staining, in the opinion of many microscopists, greatly facilitates the study of the more minute odontophores, a well-stained preparation showing the teeth as though formed of coloured glass or crystal. Although many stains are used by microscopists, the Eosin-Hæmatoxylin process, as practised by Mr. E. W. W. Bowell, being practically permanent and so excellent in many ways, may be selected as a representative one.

In this process, the radula, after the final washing previously described, is warmed in water slightly acidulated with acetic acid to neutralize any trace of alkali left in the preparation; it is then dehydrated with absolute alcohol, placed upon a clean excavated slide, and Ehrlich's undiluted Hæmatoxylin applied for two or three minutes; should the blue stain, after its development by washing in tap water, prove to be too strong, the fault is quickly corrected by a momentary sojourn in alcohol or water faintly acidulated by Hydrochloric Acid.

The Hæmatoxylin stain acts by outlining the basal plates and staining the edges of the structures generally, and is strengthened and assisted in emphasizing important details and more especially the cones, by the use of a saturated aqueous solution of Eosin, which should be used for five or ten minutes, after which dehydrate with absolute alcohol through cigarette paper and clear with oil of cedar, then arrange the object on the slide, dry off the clearing agent with cigarette paper, and put a drop of Canada balsam, preferably in Xylol, on the object, and then place the cover glass in its position and complete by cementing.

The ŒSOPHAGUS (ὄισω, I shall carry; φαγεῖν, to eat) or Gullet, is a ciliated tube of variable length, thickness, colour, and markings in the different species, and which, though sometimes flexuous and in *Neritina* even sinuous in character, usually has an almost direct course extending in the Gastropoda from the pharynx to the stomach, but in the Pelecypoda originating at the oral orifice owing to the absence of pharyngeal specialization. Its limits are ill defined, due to the imperceptible change in its structure and capacity, the walls being very distensible owing to the longitudinal folds into which they are thrown. Interiorly it is lined with cylindrical and partially glandular epithelium, and exteriorly by muscular layers, whose successive contractions impel the food onwards towards the stomach, before reaching which the tube may expand to form one or more distinct enlargements, separated by more or less definite constrictions, corresponding to and indicating division of function.

FIG. 544.—Various cells from the œsophagus of *Helix pomatia* L., highly magnified (after Vogt and Yung).

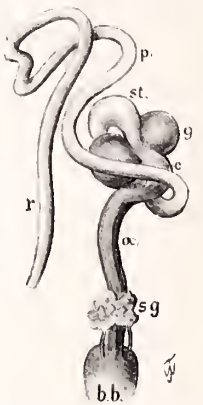


FIG. 545. — Alimentary canal of *Limnæa peregra* Müll., × 4, showing the relative positions of the crop, paired gizzards, stomach, etc.

b.b. buccal bulb; *c.* crop; *g.* paired gizzards; *st.* stomach; *p.* plecton; *r.* rectum; *æ.* œsophagus; *s.g.* salivary glands.

The CROP, the most anterior of the œsophageal enlargements, acts as a kind of reservoir or preliminary receptacle for the ingested food, and is a large and fusiform thin-walled sac, often conspicuous by the colour of its contents, occupying the front of the visceral hump in the testaceous species and filling a considerable part of the body cavity. The lining membrane resembles the œsophagus

in being thrown into a series of distensible longitudinal folds, visible through the thin walls and giving the organ a striated appearance. In *Testacella* and probably other species, the crop may acquire stronger and more muscular walls and assume the functions of the true stomach by carrying on the processes of active digestion therein.

The Gizzards or organs for the mechanical grinding of food are present in some species and placed on the foregut between and partially beneath the crop and the stomach. In *Limnæa* they consist of two globular and laterally paired purple-brown muscular pouches formed by an excessive local development of the muscular investment of the œsophageal tube, and are usually partially filled with sand or gravel to assist in the crushing and trituration of the food before undergoing the process of digestion within the true stomach, as it is only posterior to such muscular enlargements that the true digestive ferments are encountered.

The four cavities, the crop, the paired gizzards and the stomach, thus concerned in the storage, trituration and digestion of food really form only a single chamber with four recesses, and bears a general external resemblance to the Quatrefoil of Gothic architecture or may be likened to the nave and transept of a cathedral, the lateral gizzards representing the transepts and the crop and stomach the nave of the building.

The Salivary Glands (*saliva*, spittle), whose presence in the mollusca is apparently correlated with the development of a pharynx, and which do not therefore exist in the Pelecypoda, except perhaps in such archaic genera as *Nucula*, etc., in which there are paired glandular pouches opening into a vestigial buccal cavity, which may represent the early form of these organs, that of a pair of simple tubules, with the secretory part located at the distal end, as in *Actæon* and other archaic Gastropods. The organs of Semper, which I have regarded as more especially gustatory in function, are considered by many to be homologous with and to represent the Buccal or Anterior Salivary Glands present in the Cephalopoda, Amphineura and other groups.

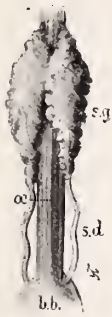


Fig. 546.—Salivary glands of *Helix hortensis* Müll., × 3, showing the character and mode of apposition to œsophagus.
b.b. buccal bulb; *œ.* œsophagus; *s.g.* salivary glands with their ducts, *s.d.*

In the Gastropoda, the salivary glands arise as simple outgrowths of the alimentary canal, and are paired foliaceous lobulate organs, often fused together dorsally, composed of branched blind tubules lined with glandular epithelium and attached by connective tissue to the sides of the œsophagus or to the walls of the foregut or crop, and though there is a general resemblance in this organ among the different species, yet there are some divergent forms, the most striking example being *Cyclostoma elegans*, whose salivary glands in their natural position are curiously coiled up, but when unfolded resemble the handles of church-bell ropes.

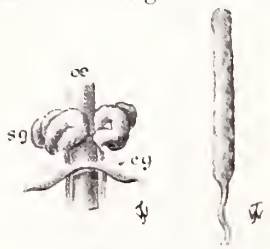


Fig. 547. Fig. 548.

Fig. 547.—Anterior part of œsophagus of *Cyclostoma elegans* (Müll.), × 3, showing the disposition of the Salivary glands. *c.g.* cerebral ganglia; *s.g.* salivary glands; *a.* œsophagus.

Fig. 548.—Salivary gland of *Cyclostoma elegans* (Müll.) opened out.

The secretory cells are large and somewhat oval, with large oval nuclei, which can be rendered visible by reagents; they are invested by connective tissue, containing free nuclei. The secretions escape from the individual cells by the rupture of their investing tissue, and are gathered eventually into the usually darkly pigmented common ducts of each gland, which are placed at each side of, and accompanying the œsophagus through the nerve ring, and convey the fluid into the upper part of the buccal cavity, where it is discharged by enlarged outlets.

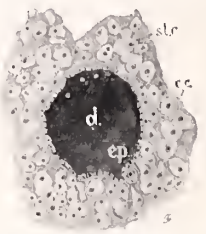


Fig. 549. — Transverse section through Salivary gland to show the arrangement of the cells, highly magnified (after Vogt and Yung).

sl.c. nucleated salivary cells; *c.c.* scattered connective tissue cells; *d.* lumen of duct of gland, showing some of the more minute duct endings; *ep.* epithelium.

The constituents of the salivary secretions differ in the different groups, some marine genera even secreting sulphuric or hydrochloric acid, but the Gastropoda of our country usually secrete a ferment which, in addition to mixing with and moistening the food and thus assisting its passage along the digestive canal, also converts the starch of the food into glucose or sugar. In our branchiate species these secretions have been ascertained to contain Calcium, Mucin, Sulphocyanate and Calcium-phosphate, and possibly a trace of Chlorine, while in the Pulmonates, Calcium and Chlorine are the chief constituents, Sulphocyanate and Calcium-phosphate being doubtfully present.

The Stomach or mid-intestinal sac is a specialized enlargement of the digestive tube, in or near to which the chief digestive processes are performed and whose walls are often thickened and strengthened by constrictor muscles, and although, in many species, the stomach seems blended morphologically and functionally with the crop, the two organs are often perceptibly distinct. It is usually of an elongate or ovoid form, but, being placed at and forming the termination of the first alimentary tract, it is often so bent and curved as to seem a lateral outgrowth of the alimentary tube, the cardiac or œsophageal and the pyloric or intestinal apertures becoming more closely approximated in proportion to the abruptness of the angle formed by the returning tract.

Fig. 550. — Epithelial cells from stomach of *Helix pomatia* L., highly magnified (after Vogt and Yung).

Fig. 551. — Interior of stomach of *Cyclostoma elegans* (Müll.), × 4, showing its complicated and sacculate walls (after Garnault).

œ. œsophagus ; *i.* intestine ; *d.g.* digestive glands and ducts.

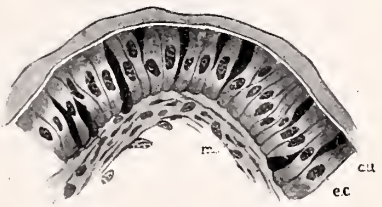


Fig. 552.—Section through the walls of the stomach of *Helix pomatia* L., highly magnified (after Vogt and Yung).

cu. cuticle ; *e.c.* cylindrical nucleated epithelial cells with interposed lacunæ ; *m.* muscular layer with nucleated connective tissue.

Interiorly the walls of the stomach are beset with glands secreting a digestive fluid and thrown into longitudinal folds continuous with those of the œsophagus and often crossed by more indistinctly transverse ones, giving the stomach a somewhat sacculate aspect. There is often a cœcum or accessory sac on the right side in the pyloric region, the Stylotheca (στυλος, a rod; θηκη, a receptacle), which may extend between the convolutions of the intestines, and contains the

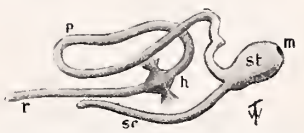


Fig. 553.—Alimentary tract of *Dreissensia polymorpha* (Pall.), more especially to illustrate the position and character of the Stylotheca (after Moquin-Tandon).

m. mouth ; *st.* stomach : *p.* plecton ; *r.* rectum piercing the heart, *h.* ; *s.c.* pyloric cœcum or stylotheca.

crystalline style. In some species, this sac can be shut off from the stomach by a valve, or, as in *Unionidæ* and other groups, may become fused with the initial part of the intestine, communicating therewith by a narrow slit.

The Flèche-tricuspide or three-pointed body is a firm and gelatinous cuticular investment of the internal walls of the stomach, especially developed towards its pyloric end and even continued within the intestine itself. This stomachal coating, which is continuous with the crystalline style, especially characterizes the Pelecypoda, but is present in many Gastropods, and is secreted by the epithelium of the stomach, chiefly for the protection of its delicate walls and the secretory cellules therein, but in certain marine genera this structure may become differentiated to form variously shaped masticatory plates.

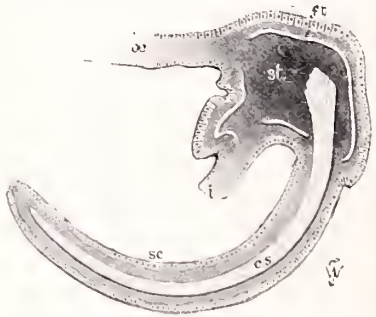


FIG. 554.—Median section through Stomach and Stylotheca of *Donax*, showing the Crystalline Style *in situ* and the arrangement of the Flèche-tricuspide on the stomach walls, greatly magnified (after Barrois).

st. stomach, with the Flèche-tricuspide *f.t.*; *æ.* œsophagus; *i.* intestine; *sc.* Stylotheca, with the contained and projecting Crystalline Style *c.s.*

The Crystalline Style, formerly supposed to be correlated with the absence of mandibles, is a semi-transparent variously shaped rodlet of concentric structure, continuous with and of similar consistency to the Flèche-tricuspide, of which it is a specialized outgrowth, usually projecting freely into the cavity of the stomach from the pyloric cœcal sac, secreting and containing it. It bears some general resemblance to a pestle and mortar, and probably assists to more intimately intermix the food in the stomach with the gastric ferments, which are usually poured directly into the stomach from the digestive gland in those species possessing the crystalline style, but where the pyloric sac is not developed the digestive fluid may be emptied into the plecton, whose restricted diameter allows a thorough intermixture to readily take place. The stylet and its extensions being exposed to the action of the digestive fluids become softened and partially dissolved, furnishing the material for surrounding with a soft glutinous film any sharp, angular particles accidentally swallowed with the food, thus

FIG. 555.—Crystalline Style of *Anodonta cygnea* (L.), greatly enlarged (after Moquin-Tandon).

preventing the laceration of the walls of the stomach and intestines, and facilitating the passage from the body of the irritant objects.

These protective developments are, however, not persistent organs, but disappear and are renewed periodically, probably forming during times of plentiful food supply, and disappearing when a prolonged scarcity of food has led to their absorption by the animal, in a similar way to that in which other animals absorb superabundant tissues during periods of famine.

The Digestive Gland, perhaps better known as the liver, is the active organ of digestion and is a large brownish or greenish organ, partially or entirely enveloping the stomach and adjacent organs, more especially in the Pelecypoda, in which it is more developed than in the Gastropoda, an increased size of the digestive glands being often correlated with a reduction in the extent of the gut.

The organ is usually formed by two chief, but unequal, lobes, the left lobe being larger than the right, this asymmetry being apparent from the first development or rapidly becoming so, except in *Neritina* and *Valvata*, in which they are equal and symmetrical during development. It consists of innumerable acini, cleft into digitiform processes or cœca, which are aggregated into lobules of varied size and complexity, bound together and surrounded by connective tissue and usually encompassed by a plexus of delicate blood vessels, which in *Arion ater* and other species are opaque milk-white showing strikingly against the dark background, while externally the whole gland is surrounded by a blood sinus. There is an outer structureless membrane, and internally the organ is chiefly composed of three kinds of cells, viz., ferment cells, liver cells and lime cells. The ferment and liver cells enclose granules of fat, albumen and pigment and differ chiefly physiologically. The lime cells, which contain phosphate or carbonate of lime, are

Fig. 556.—Digestive tract of *Limnæa stagnalis* (L.), × 2, showing the digestive gland and its ducts.

b.b. buccal bulb; *s.g.* salivary glands; *œ.* œsophagus; *c.* crop; *g.* gizzards; *st.* stomach: *d.gl.* digestive gland and its ducts; *a.* anus.

plentiful in many groups, but greatly reduced in number in the Limnæidæ and scarcely present in *Succinea*; they probably represent a store of calcareous matter to be utilized in the growth of the shell or the formation of the epiphragm.

The ferment is a rather thin dark yellowish fluid, decolorized and dissolved by Nitric Acid, and is probably a derivative of hæmatoidin. It is conveyed by the tiny lobular ducts which gradually unite together and finally enter the stomach anterior to the pyloric cœcum, when present, but otherwise, usually behind the stomach and into the initial part of the intestine, by one or more, but usually by two chief ducts; in some cases, as in *Cyclostoma*, the ducts may bear isolated acini, which have been considered as pancreatic cœca, although such developments in the Cephalopoda have been shown to correspond in function with the salivary glands of the higher Vertebrates.

The digestive gland functions chiefly as a pancreas, but there are reasons for regarding it as also possessing hepatic functions. The peptic ferment is stated to be identical with Krukenberg's Helicopepsin, while the diastatic ferment, which disappears during hibernation, is stated to be capable of dissolving raw starch, but has no action on cellulose. The fat emulsifying power also disappears in winter.

In the Pelecypoda generally the digestive gland has been ascertained to contain Diastatic ferments, Pancreatin, Peptones and doubtfully Glycogen, while in Gastropoda the contents are similar with the addition of Sodium. But the precise constitution of the Gastropod liver, as exemplified in *Helix pomatia*, is, according to Dr. Levy, by alcoholic extract, Enterochlorophyll, Lecithin, Oleic and fatty Acids, and as ash, Chlorine, Phosphoric and Sulphuric acid. The aqueous extract yielded Sugar, Glycogen, Sinistrin, Globulin coagulating at 66C, Hypoxanthin and other bases precipitable by phototungstic acid, and as ash, Potassium, Sodium, Calcium, Magnesium, Manganese, Chlorine, Phosphoric and Sulphuric acids, with traces of iron. In winter silica was also found as an ash constituent. The ethereal extract yielded only a trace of fat.

Glycogen ($C_6H_{10}O_8$) or, as it is sometimes called, Liver-sugar, is a white amorphous amyloid substance, insoluble in alcohol or ether, and when dissolved in water exhibits a strong dextro-rotatory influence on polarized light, and is distinguished by its power to change to sugar or glucose in the presence of animal ferments. It is found

in most of the tissues of many mollusks, but is more especially found in the digestive gland, making its appearance therein about 17 hours after feeding and disappearing entirely after one to three days' fasting. It forms 1·75 per cent of the digestive gland in *Helix pomatia*, decreasing during hibernation to 0·429 per cent. It would appear to be formed more especially from starchy food and is probably a respiratory fuel substance, as it disappears from the blood after its oxygenation in the respiratory organs, and is present in the muscles in a ratio inverse to their activity.

The Intestine, or gut, which arises at the stomach and terminates at the anus, has its inner epithelial layer overlaid by a film of closely adherent connective tissue, with numerous glandules together constituting the mucous membrane. Exterior to this combined layer is the muscular stratum, whose contractions serve to impel the food on its course through the digestive canal. The intestine is greatly varied in its length and mode of convolution in the different groups and even in the different species, but there is no distinct division into large and small intestinal tracts as in the vertebrates, although the relative size of the parts may be reversed in many species, the pyloric end being often the largest.

Fig. 557. — Ciliated and other cells from the lining membrane of the intestinal canal of *Helix aspersa* Müll., highly magnified (after Howes).

The two largest were actively secretory.

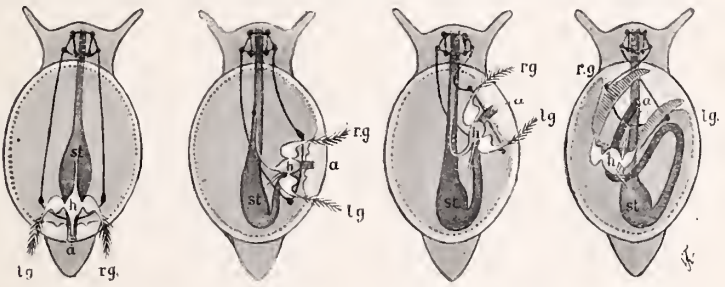


Fig. 558. Fig. 559. Fig. 560. Fig. 561.

Figs. 558-561.—Diagrammatic figures showing the mode in which the chief intestinal flexure has originated (after Butschli). *st.* stomach ; *a.* anus ; *r.g.* right gill ; *l.g.* left gill ; *h.* heart.

The spiral twisting undergone by the visceral sac of most Gastropods during the progress of body torsion, has necessarily involved in its movement the intestinal canal and other organs contained therein, and it is remarkable that in some of our nude forms, as the genera *Amalia* and *Arion*, the whole of the internal organs

behind the shield still retain a very considerable twist, equal to about one and a half spiral turns and recalling the similar twisting exhibited by the internal organs of *Buliminus*, and yet, except the lateral position of the organic orifices, there are no external evidences of their spirally coiled viscera, and it forms an unexpected corroboration of the former possession of a spiral shell by these groups.

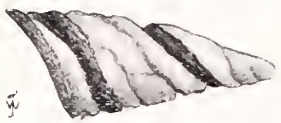


FIG. 562. — Hinder end of body of *Amalia sowerbyi* (Fér.), with integument removed, showing the spirally twisted digestive gland and intestinal tract, × 2.

The Intestinal canal may be conveniently divided into two sections, an anterior section, the Plecton, which is usually more or less complexly convoluted, and a straighter terminal one, the Rectum.

The PLECTON (πλεκτον, twisted or twined) originates upon the ventral side of the stomach, from which it is sometimes separated by a sort of valve, and in the herbivorous and omnivorous species is often very long and complexly convoluted, a feature which has arisen chiefly by the elongation of the primitively straight and simple canal; the coiling exhibited is, however, never continuous in one direction, like a watch-spring, but is reversed from time to time, so that the tracts considered as convex are practically equalled by others bent in an opposite direction and forming what is known as a "reversed spiral," an arrangement which always takes place when a lengthening body with fixed ends is confined within a limited space.

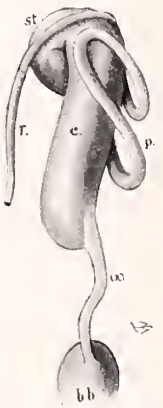


FIG. 563.—Alimentary tract of *Succinea elegans* Risso, × 5, Exminster Marshes, Devon, collected by Mrs. Smith, showing the character of the plectonic and rectal tracts.

b.b. buccal bulb; *œ.* œsophagus; *c.* crop, blending with stomach *st.*; *p.* plecton or coiled intestine; *r.* rectum.

The Plecton, though continuing the digestive processes set up by the stomach and also receiving the secretions of the digestive gland in those species not possessing the crystalline style, is chiefly absorptive in function, this process being facilitated by the development on the ventral side of the intestinal tube, especially in the earlier part of its course, of a strong infolding of its walls, which greatly increases the absorptive surface and forms what is known as the Typhlosole. This absorption of the nutritive products of digestion from the alimentary tract is not accomplished

by special organs, as in Vertebrates, but is effected by endosmosis through the intestinal walls into the blood contained within a plexus of blood vessels distributed over the whole surface of the alimentary canal and is thence carried by the blood to every part of the body, the functions of digestion, absorption and circulation being thus closely united.

FIG. 564. — Portion of intestinal canal of *Testacella haliotidea* Drap., showing the plexus of blood vessels upon its surface, highly magnified after Lacaze-Duthiers).

The RECTUM (*rectum*, straight) is the straight terminal section of the intestine, and often differs in colour and character from the preceding convolute portion, being sometimes more muscular and palpably thicker and sacculate, as in *Planorbis corneus*, or may be more slender, as in the Limaces. In our Pelecypods, in *Neritina* and other of the more primitive Streptoneura, the rectal tube in its course towards the exterior is embraced by the ventricle of the heart, but in *Viviparus* the pericardium only is pierced and in other groups every gradation is found leading to the final freedom of the rectum from all contact with the heart.

The rectum bears upon its outer side a band of longitudinal muscular fibres which retract the collar, thus shortening the rectal tube and expelling the contents in various forms, according to the species and to some extent according in colour with the nature of the food. Ordinarily the excrementitious matters are expelled in a vermicular or twisted shape or they may, as in *Cyclostoma*, assume a spherical form. The anus or excretory orifice is closed by a kind of sphincter muscle, and being always in association with the respiratory cavity, if one be present varies its position with the breathing organ, but its termination always lies in the path of the excurrent stream, if a special one is present. In the Pelecypods it is placed at the hinder end of the body above the posterior adductor, but in most Gastropods it opens more or less anteriorly, in dextral specimens upon the right side of the body and in sinistral individuals on the left, and is sometimes placed upon the fæcal lobe, a small and slightly twisted outgrowth, which in *Planorbis* has a rich vascularization. In *Testacella*, whose visceral coil has become untwisted by the detorsion of the body, the anus has reverted to its primitive posterior position.

FIG. 565.— Respiratory orifice of *Agriolimax agrestis* (L.), showing the anterior anal cleft, × 3.

The Rectatheca (*recta*, straight: *theca*, a sheath), a remarkable blind diverticulum, arises about midway in the course of the rectum and extends backwards above the stomach in certain of our nude species, but its significance or function is unknown, although in Birds analogous structures have been correlated with the function of digesting chitin and cellulose, and it is probable that this is also its function in slugs, as fungi, which are mainly composed of cellulose, are a favourite food with the species possessing the cœcum. *Arion ater* is also stated by Simroth to possess a cylindrical cœcum, situate behind the hepatic ducts, which he regards as probably possessing special digestive power, and thus may be analogous in function to the Rectatheca.

Fig. 566.—Alimentary tract of *Limax flavus* L., showing the large intestinal cœcum or Rectatheca, × 2.

b.b. buccal bulb; *c.g.* cerebral ganglia; *cr.* crop, blending with the stomach *st.*; *a.* anus; *c.m.* intestinal cœcum or Rectatheca.

Our British species may be provisionally separated into three groups, viz. :—Dichodroma, Triodroma and Pentadroma, which are based upon the number of tracts the intestinal canal exhibits, although the tracts in all the groups vary greatly, not only in their length, but in the number and direction of their subsidiary flexures.

The Triodroma (τρι-, three; δρομος, a tract), which is the prevailing type of intestinal convolution in our British species, possesses only three chief intestinal tracts beyond the stomach, the first loop being

Fig. 567.—Alimentary tract of *Helix lapicida* L., × 4, as exemplifying the section Triodroma.

always ventral to the stomach and having a forward course, which is considerably varied in detail in the different species, but usually ascending above the œsophageal tract where the first anterior loop is formed, which in the Euthyneura is held in position by the cephalic branch of the aorta, afterwards passing more or less diagonally backwards and there bending forward to the rectum.

The DICHODROMA (δι-χῶς, double; δρομος, a tract or course) comprise those species in which the intestinal tracts have become reduced to one forward and one backwardly directed section; the detorsion the viscera has been subjected to having merged together the rectum and

FIG. 568.—Alimentary tract of *Testacella haliotidea* Drap., enlarged, exemplifying the section Dichodroma.

the posteriorly directed plectonic tract, this process also uncoiling the cephalic artery from its sustaining position around the anterior intestinal loop.

The PENTADROMA (πέντε, five; δρομος, a tract) show five tracts or courses beyond the stomach and, as in the Triodromous species, have the first anterior intestinal loop encircled by the cephalic artery;

FIG. 569.—Alimentary tract of *Limax maximus* L., exemplifying the section Pentadroma.

the two additional tracts in *Limax maximus* and its immediate congeners have the additional anterior loop passed around the pharyngeal retractor, which being affixed to the dorsal integument holds this loop in its proper position, the final backwardly directed tract bending in the rear to join the final tract or rectum.

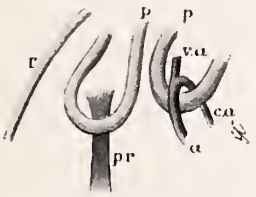


FIG. 570.

FIG. 571.

FIG. 570.—Anterior folds of the intestinal tract of *Limax maximus* L., showing how the coils are held in their anterior position.

p. plecton; *r.* rectum; *a.* aorta dividing into *v.a.* visceral artery and *c.a.* cephalic artery, the latter encircling the first anterior coil; *p.r.* pharyngeal retractor, holding the second coil in place.

FIG. 571.—Side view showing the pharyngeal retractor encircled by the second anterior intestinal coil and its attachment to the dorsal integument.

p. the second anterior coil of the plecton; *p.r.* pharyngeal retractor fixed to dorsal integument *b.*

The FOOD of the Pelecypoda consists chiefly of Infusoria and the various floating microscopic organisms brought to them by the currents produced by the ciliary investment of the branchiæ and other

organs, although this method only allows a purely passive selection of the nutrient particles to be made. The more active Gastropoda, however, often exercise great discrimination in the selection of their food, although their tastes are not identical with our own, except perhaps in their fondness for saccharines, most species being partial to the sweet parts of plants. In other respects our tastes are different; *Chærophyllum temulum*, though relished by many snails, produces unpleasant sensations on the human tongue, while many papilionaceous or pea-like plants, pleasant or merely insipid to ourselves, are carefully avoided by snails or only nibbled under stress of hunger. Although many Gastropods are more or less omnivorous, yet some species retain or have acquired a special power of feeding upon certain plants, which are adequately defended against others not similarly modified.

Plants, being the staple food of mollusks, would be much more severely ravaged by them if their constant attacks during countless ages had not contributed to develop a variety of protective devices, probably most formidable in those plants which formerly suffered most severely from their depredations. These acquired defences are now so universally present that Stahl has not found a single phanerogam unfurnished with some means of protection, rendering such plants more or less unpalatable or difficult of access, so that only dire necessity compels the omnivorants to feed sparingly upon the least protected parts of the less perfectly defended species, and although *Arion ater* and *Agriolimax agrestis* are so pre-eminently omnivorous and greedy that few plants are altogether safe from their attacks, yet even their ravages are infinitely reduced in extent by the varied obstacles to be overcome before the desired food is obtainable.

These barriers are indeed often so insuperable that certain sensitively organized species feed by preference upon dead or decaying leaves, probably thus exhibiting their keen susceptibility to the chemical protection so many plants enjoy, a protection which, being dissipated on the fall of the leaf, enables them to be then partaken of without injury.

Cultivated plants alone are not adequately armed, having probably lost by selective culture the repellant substances or structures to which they owed their preservation in a wild state, so that they are now greedily devoured by snails and slugs, and owe their continued existence in their present form solely to man's protection.

The Defensive Devices of plants operative against snails may be mechanical or chemical, and although it is difficult to recognize a close

connection between a definite group of animals and the protective arrangements of certain plants, yet such reflex contrivances undoubtedly exist, although the same protective devices may be operative against very diverse animals. Certain groups of plants are, however, distinguished by the predominance of a certain mode of protection, although few have the same protection in all their parts, flowers having usually different defensive devices to the vegetative portions, and the internal protection when present differs in character from that of the exterior.

The STRUCTURAL Defences embrace a prickly or hairy investment, and the hardening of the stems and foliage by the silicification or calcification of the more exposed tissues, and such plants are probably still acceptable to molluscan palates when their external defences can be overcome.

The Silicification of the exterior of many of our grasses, Horsetails (Equisetaceæ) and Cyperaceæ not only gives rigidity and firmness to the plants, but is a real protection against snails, helicine teeth being practically helpless against the defence it offers; its efficiency is shown in some tropical grasses, in which this silicification is so pronounced as to render them totally unfit even for feeding cattle.

Mosses are also protected by their highly silicified tissues, shown in the stiff pointed hairs, serrate margins and rough capsule stems, features particularly noticeable in *Funaria hygrometrica*.

Calcification of the tissues is the defence of many plants, and this protection may be internal and due to the deposition of carbonate of lime within the cells, *Erysimum cheiranthoides* being rendered so hard from this cause that it is avoided by even *Agriolimax agrestis*, whereas *Chara* and other aquatic groups are calcified externally, assuming an equally protective incrustation of the same substance.

Oxalate of lime is abundant in the outer tissues of Orchids, Amaryllids, Narcissi, *Typha latifolia*, *Arum maculatum* and other plants, and generally exists in the form of Raphides (ραφε, a needle), minute, needle-like crystals, $\frac{1}{100}$ to $\frac{1}{200}$ of an inch in length, which are always most plentiful near the surface and confer comparative immunity against attacks by snails and many other animals, as they wound the palate and cause a strong burning sensation within the mouth of any creature attempting to feed upon the plants containing them; they have also been known to give rise by contact to a form of eczema, even in human subjects.

The CHEMICAL Defences are constituted by more or less nauseous secretions, most abundant in the parts most liable to attack and due to bitter principles, tannin, acrid juices or exudations, essential and volatile oils, alkaloid, mucoid, or gelatinous secretions and by other obnoxious substances as yet undetermined.

Tannin or Tannic Acid exists in the epidermal cells and hairs of ferns, roses, geraniums, ericas, papilionaceous and leguminous plants, and is a very powerful protective ; many compositæ are also exceptionally rich in this substance, to which they owe their disagreeable smell, while to *Valisneria*, *Hydrocharis*, *Potamogeton* and other aquatic plants it gives partial protection, supplemented in many cases by the deposit of numerous raphides ; while in the freshwater algæ belonging to the genera *Vaucheria*, *Spirogyra*, and in Confervæ, etc., it exists in such quantities that a good ink can be prepared from the alcoholic solution of their chlorophyll.

Acrid juices are repugnant to snails and therefore the sap of *Rumex*, *Oxalis*, etc., efficiently protects these plants from many snails. Essential oils also safeguard the plants containing them, the gallic oil of the Allium tribe, the essential oils of *Ruta* and the Labiatæ conferring an immunity from attack by most species. The Willow-herbs receive a certain amount of protection from the acrid volatile oil secreted by the glandular hairs, while the Alkaloids present in the Solanaceæ and the bitter principle characterizing the Gentians perform the same duties to the plants secreting them.

Mucoid and gelatinous secretions or excretions, when well developed, are also an efficient barrier against snails. *Nitella syncarpa* secretes a gelatinous investment which acts as a strong deterrent to *Limnæa stagnalis* and probably other species, while *Collema granosum*, a gelatinous lichen, is left untouched by both land and fluviatile snails.

These various defences render it probable that the mollusca though, apparently, living in the midst of plenty are often in reality only able with difficulty to eke out a precarious existence. This is confirmed by the exhaustive experiments upon various snails carried out by Mr. Gain, which demonstrated, for example, that out of 192 varieties of food—chiefly the commoner plants of the vicinity of Newark, Notts.—offered to a colony of *Helix hortensis*, no less than 139 were apparently so efficiently protected that they were quite untouched and 17 others only slightly nibbled, even after definite periods of starvation. Of the 36 remaining foods more or less freely partaken of, 21

were cultivated plants and 4 were fungi, and only the residuary 11 were wild phanerogamic plants, but 6 of these were not very freely eaten and not one was devoured with that avidity which characterizes snails when really pleasant food is offered, for at such times they consume enormous quantities, eating the night through without intermission, *Agriolimax agrestis* having been known to devour one-third its own weight within twenty-four hours, and when we see the destruction wrought amongst plants defended in such various ways, we must conclude that many would soon be entirely extirpated if the barriers to their free consumption were removed.

The Circulatory or Vascular system, known also as the Hæmocœl (αἷμα, blood; κοῖλος, hollow), is greatly developed in the mollusca, and consists of blood vessels and sinuses, shut off from the general digestive cavity, of which it may, however, be regarded as an adjunct, as it is the medium by which nutriment is absorbed from the alimentary canal and carried to all parts of the body.

A portal circulation is constituted by that portion of the systemic circulation of the blood which flows to and circulates within the kidney or renal organ prior to entering the auricle.

The Pericardium (περί, around; καρδια, heart) is a thin-walled sac, often thick and glandular in front, which contains or encloses the heart, and is partially embraced by the renal organ. It is constituted by an isolated part of the secondary body cavity or cœlom, whose epithelial lining also extends over and covers the exterior of the heart. The pericardial cavity receives the acrid secretion of the pericardial gland which is passed from the system by way of the reno-pericardial funnels.

The Heart is the central and chief blood vessel, and is a dorsally placed contractile organ, symmetrical and median only in Pelecypods and in the most archaic Gastropods. In those Gastropods whose viscera have been most modified in position by the torsion and subsequent partial detorsion the body has undergone, the heart, in dextrally coiled individuals possessing a respiratory cavity, occupies the left anterior side of the body, but is placed at the right side in sinistral specimens, and it is only when detorsion is complete that the heart

Fig. 572.— Heart of *Helix virgata* Da Costa within the opened pericardium and also showing the close apposition of the renal organ or kidney.

a, auricle; *v*, ventricle; *k*, kidney or renal organ.

again occupies its more primitive position at the rear of the animal; always, however, maintaining a close proximity to the respiratory organs, though not placed, as in fishes, between the veins of the body and the branchiæ, but between the arteries and the respiratory organs, receiving therefrom the vitalized blood, which it propels through the system, and hence is called an arterial or systemic heart. Interiorly the heart is variously chambered, but its walls are destitute of any endothelial covering, so that the muscle fibres are in direct contact with the blood.

Fig. 573. Fig. 574. Fig. 575.

Diagrams illustrating stages in the development of the pericardium and heart in *Sphærium corneum* (L.), (after Ziegler).

Fig. 573.—Early stage of development, showing the paired pericardial vesicles and nascent auricles.

r. rectum, entirely free from the pericardial vesicles; *p.p.* paired pericardial vesicles at each side of, but distinct from the rectum; *a.a.* invaginations of lateral walls of pericardial vesicles forming the rudiments of the auricles.

Fig. 574.—Intermediate stage, showing the formation of the ventricle as two separated chambers.

r. rectum, now enclosed by the ventricles; *a.a.* auricles; *v.v.* paired rudimentary ventricles, separated by a median septum, and not yet forming a single vessel; *p.p.* pericardial cavities.

Fig. 575.—Heart showing the fusion of the paired pericardial and ventricular cavities, owing to the absorption or loss of their dividing septa.

r. rectum, now surrounded by ventricle; *a.a.* auricles; *v.v.* ventricle, now constituted by a single cavity; *p.p.* pericardium.

The heart is constituted by two or more connected chambers, known according to the function they discharge, as Ventricles and Auricles.

The Ventricle (*ventriculus*, diminutive of *venter*, the stomach; the old anatomists were in the habit of terming any small cavity or dilatation furnished with an inlet and outlet a "Ventricle," *i.e.*, a little stomach) is typically a median longitudinal vessel, usually innervated by the abdominal ganglia, which by its powerful wave-like contractions forces through the body the blood received from the auricles. It is often obconic in shape, with the cavity enclosed by thick, opaque and muscular walls, formed of granulated unstriped muscle-fibre thickly felted together and supported internally by a number of muscular pillars or *columnæ carneæ*, and is probably derived from a much more ancient arrangement, in which there was a pair of longitudinal blood vessels, one at each side of the centro-dorsally placed rectum, which gradually

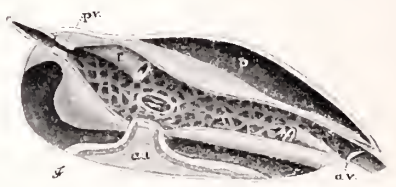


Fig. 576.—Ventricle of *Anodonta cygnea* (L.), × 2 (after Rankin), laid open, showing the internal valvular arrangements and the enclosing pericardium.

an. auricle; *a.v.* anterior ventricular valve; *p.v.* posterior ventricular valve; *r.* rectum.

united in the median line to form a common propulsive vessel, enclosing the rectum between their walls.

The Auricles (*auricula*, diminutive of *auris*, the ear; the auricles in man being said to resemble the external ears of some quadrupeds) are generally pyriform, thin and transparent, with few muscle-fibres, usually innervated by the pallial ganglia, and often smaller than the Ventricle, especially in the Pulmonata; they receive the blood direct from the respiratory organs and discharge it into the ventricle by a slender neck, its reflux being prevented by the auri-ventricular valves at the junction. Valvular contrivances may also be present in various other parts of the system, more especially in connection with the different turgescible organs, as the foot, tentacles, siphons, etc. The number of auricles varies in correlation with the number of respiratory organs, the Pelecypoda always possessing two symmetrical auricles, corresponding to their paired branchiæ, but in our Gastropoda they are reduced to one only, owing to the loss of the primitively left branchia. The contractions and dilations of the auricles, when paired, are always simultaneous, and in every case alternate with those of the ventricle.

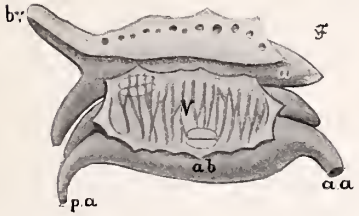


Fig. 577.—Heart of *Patella* with the ventricle laid open, to show the muscular pillars or *columnæ carneæ* and the valvular openings to the auricle and to the arterial system, greatly enlarged (after Wegmann).

v. interior of ventricle with the vertical *columnæ carneæ* and showing the valve of the auricle to the left and the aortic valve towards the base; *b.v.* branchial vein, also showing the openings through which the blood from roof of pallial cavity enters the auricle; *a.* auricle; *a.a.* anterior aorta; *p.a.* posterior aorta; *a.b.* aortic bulb.

Fig. 578.—Transverse section through the heart of *Anodonta cygnea* (L.), × 2 (after Rankin), showing the structure of the walls of the ventricle, the arrangement of the auricular valves and the position of the rectum.

au. auricles; *v.* rectum; *ty.* typhlosole.

The number of auricular chambers to the heart has formed a basis for the grouping of the mollusca in two sections, Diotocardia and Monotocardia, which, like other structural details, are also of value as showing phylogenetic relationship.

The Diotocardiate (δύω, two; ὦτα, auricles; καρδια, heart) heart is characteristic of the Pelecypoda and Zygobranchiate Streptoneura, and is composed of a pair of symmetrically disposed lateral auricles and a single ventricle, which is often pierced by the rectum, and though the most complex is the more primitive form.

The Monotocardiate (*μόνος*, single ; *ὦτα*, auricles ; *καρδια*, heart) heart more especially characterizes the Pulmonata, in which the organ is larger than in the Azygobranchiate Streptoneura, which also possess it; although the most simple form, it is a simplicity derived from the more complicated Diotocardiate organ, and consists of a single

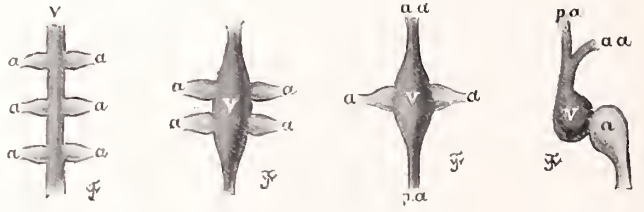


Fig. 579. Fig. 580. Fig. 581. Fig. 582.

Diagrams showing the character of the heart in various groups of mollusca and its structural relationship to the more primitive organization of the Annelids (after Gegenbaur).

Fig. 579.—Part of the dorsal propulsory vessel or ventricle of a worm with some of the lateral contributory vessels or auricles.

Fig. 580.—Heart and paired auricles of *Nautilus* showing the reduction to two pairs of auricles, corresponding to the four branchiæ.

Fig. 581.—Diotocardiate heart of a Pelecypod, showing the further reduction of the lateral auricles to a single pair in correlation with the paired branchiæ.

Fig. 582.—Monotocardiate heart of a Gastropod, showing the single auricle, its fellow having disappeared in conformity with the loss of the primitively left branchia.

a. auricle ; *v.* ventricle ; *a.a.* anterior aorta ; *p.a.* posterior aorta.

ventricle and a single auricle, the auricular reduction being correlated with the loss of the left branchiæ and also with the presence of the single pulmonary chamber.

The Circulatory vessels are usually divided into an arterial and a venous system. The Arterial system, in addition to the heart, is constituted by the aortæ, the arteries, the arterial lacunæ, and the capillaries, all conveying the blood centrifugally, or from the heart to the various organs of the body. The Venous system is composed of tubular vessels and a limited number of spacious cavities or venous sinuses, the enclosed venous blood moving centripetally or from the organs and exterior of the body towards the heart, becoming accumulated within the venous sinuses before entering the respiratory organs.

The Aorta (*ἀορτέω*, a lengthened form of *ἀείρω*, to raise or hang up, so called because it was supposed to hang up and keep in position the vertebrate heart, as indeed to some extent it does) is the main trunk of the arterial system in the mollusca and is usually short, originating at the ventricle and directly receiving the blood from it for distribution through the body. In the Pelecypoda there is usually an anterior and a posterior aorta, which arise from opposite ends of the longitudinally placed ventricle, but in our Gastropods the repre-

sentatives of the anterior and posterior aortæ of the Pelecypoda combine before reaching the ventricle, to form a single aortic vessel, their approximation and basal fusion being probably due to the body torsion the Gastropoda have undergone.

The Arteries (ἀήρ, air ; τηρέω, to keep ; the ancients believing these vessels naturally contained air) originate by the furcation of the aortæ and are of smaller calibre. In the Gastropoda one branch, dividing and redividing, traverses the body and supplies the intestinal tract, the digestive gland, the genital gland, etc., and is known as the Visceral artery, while the other, known as the Cephalic artery, bends round and supplies the head and its organs, encircling the first

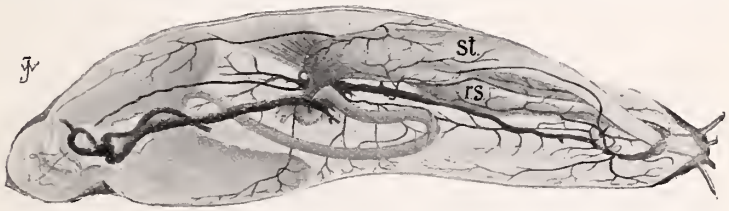


Fig. 583.—*Testacella haliotidea* Drap. laid open dorsally and the viscera partially removed to show the arterial blood vessels, × 2 (after Lacaze-Duthiers).

st. stomach ; *r.s.* radular sac ; *a.* auricle of the heart ; *v.* ventricle, from which originate the anterior and posterior aortæ and the subsidiary arterial vessels.

anterior intestinal coil and sending a strong branch to the foot. In some species, and especially in *Arion ater*, the walls of the arteries and arterioles are greatly thickened by a surrounding sheath of connective tissue, containing numerous calcareous and fatty particles, which gives the vessels an opaque, milk-white appearance, beautifully contrasting with the dark tissues upon which their complex ramifications are traced.

The arterial vessels may terminate and be joined to the venous system by finer and more delicate vessels or may open by wide funnel-shaped and sometimes contractile orifices into lacunæ.

The Lacunæ (*lacuna*, a pool), Hæmatocœles or arterial blood sinuses, are the intervening spaces which permeate between the various organs of the body ; they vary greatly in size and capacity, and are destitute of proper endothelial covering.

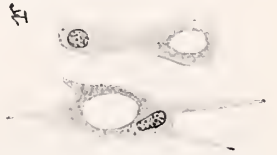


Fig. 584.—Connective tissue cells of *Arion ater* (L.), showing the origin of lacunæ, highly magnified (after Brock).

The Capillaries (*capilla*, a hair) are the minute, thin-walled blood vessels which, in some forms, constitute the terminations of the

smaller arteries and the beginning of the smaller veins; these intermediary vessels which connect together the arterial and the venous systems are distinctly developed in *Testacella* and other species.

The Veins (*vena*, blood vessel) are the blood channels which convey the blood back to the heart, whether by way of the respiratory organs or direct; they are continuous with and receive the blood from the capillaries, but gradually unite to form larger vessels, which eventually empty into the large venous sinuses preparatory to diffusion in the respiratory organs.

The Venous Sinuses, or blood reservoirs, are large cavities within which the blood, exhausted of its oxygen and loaded with the waste

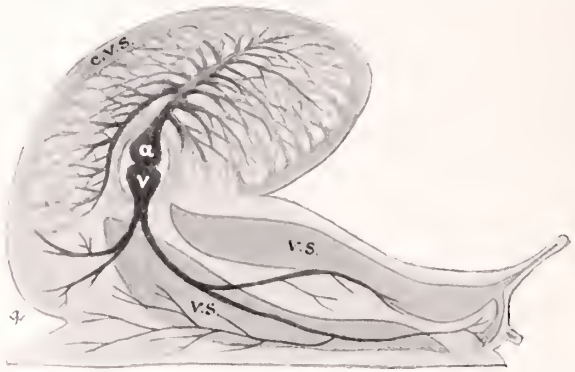


Fig. 585.—Diagram of the circulatory system of *Helix*, especially illustrating the venous sinuses (after Griffiths).

v.s. venous sinus; *c.v.s.* circular pulmonary sinus; *a.* auricle, receiving the blood after aëration in the pulmonary plexus; *v.* ventricle, giving off the anterior and posterior aortæ.

matters from the oxidation of the tissues, is accumulated after its circuit of the body, prior to entering the renal and respiratory organs for purification.

In the Gastropoda the chief venous sinuses are in the pedal and pallio-visceral regions, while in the Pelecypoda the chief venous sinus is known as the Vena-cava, and is a spacious cavity lying longitudinally beneath the pericardium.

The Blood or Hæmolymph (*αἷμα*, blood; *lympha*, water) is the circulatory fluid, and is a slightly viscous semi-transparent albuminoid fluid, remarkable for the quantity of calcic carbonate it contains, as shown by its effervescence when treated with acids. It supplies the various glands with the material from which they elaborate their various secretions and also receives the products of the oxidisation of the various tissues, conveying them to the excretory organs for

elimination from the body. Analysis shows Carbonate and Phosphate of Lime, Carbonate and Chlorhydrate of Soda, Oxide of Iron, and a trace of Oxide of Manganese to be some of the constituents of molluscan blood.

The blood may form fully half the total weight of the body in the Pelecypoda and about one-sixth in the Pulmonates, this relatively large volume enabling a portion to be utilized to protrude or stiffen different parts or organs of the body, as strikingly seen in the protrusion and extension of the tentacles in the Gastropoda and in the turgescence of the foot in the Pelecypoda, this being accomplished by permitting the inrush of blood to the particular organs to continue and retaining it therein by the action of suitably disposed sphincter muscles, the most important being known as "Keber's Valvule," whose action permits the free ingress of blood to the foot, but by the closure of the great afferent renal vein prevents its escape therefrom, thus retaining all the blood within the foot and enabling it to quickly become firm and rigid for locomotory purposes.

FIG. 586.—Keber's valvule in *Anodonta cygnea* var. *cellensis* C. Pfr., greatly enlarged (after Fleischmann).

k.v. sphincter of Keber's valvule; *r.c.* renal cavities; *pc.* pericardium; *r.p.f.* reno-pericardial funnel.

HÆMOCYANIN (*αἷμα*, blood; κυανεος, dark blue), a proteid in combination with copper, with a chemical composition of C_{867}, H_{1363} N_{223} CuS_4 O_{258}, is also usually present in molluscan blood and functions in a similar, but feebler, way to hæmoglobin, by absorbing oxygen from the air or water and carrying it to the more remote tissues of the body, the bluish or violet colour, characterizing it when rich in oxygen, being gradually lost as that substance becomes abstracted by the tissues with which it comes in contact.

HÆMOGLOBIN (*αἷμα*, blood; *globus*, a sphere), is an albuminoid in association with iron, which during respiration enters freely into an unstable combination with oxygen, from which it is again separated by the tissues as the blood circulates through the body. It is present in the buccal muscles of many species, whose energetic action calls for more active oxygenation than hæmocyanin can accomplish. The

same active respiratory substance is found abundantly in the blood of adult Planorbes, but not confined within special corpuscles, as in man or in the molluscan genera *Solen*, etc., but diffused through the circulatory fluid, to which it gives a bright pink appearance; this special abundance of hæmoglobin in *Planorbis* may be considered to be in direct correlation with the transitional character of their respiratory system and the feebly oxygenated state of the stagnant pools in which they so often live.

The Amœbocytes (ἀμείβω, to change; κύτος, a cell) or white blood corpuscles, known also as Phagocytes, are minute, indistinctly nucleated, unicellular organisms of variable size, resembling those of man in structure and exhibiting the same amœboid movements. They possess various assimilating and nutrient functions and contain more or less abundant refractive albumenogenous granules, whose protoplasm is believed to serve as a storehouse for the accumulation of fat and albuminoids and to form the means ready for the repair of wounded tissue.

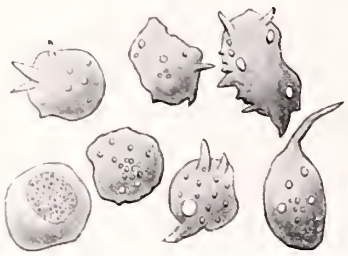


Fig. 587.—Blood corpuscles or amœbocytes of *Helix pomatia* L., fixed with osmic acid, highly magnified (after Vogt and Yung).

The Amœbocytes seem from their origin to be connective tissue cells especially adapted to live in an albuminous medium and are numerously present in the blood; they originate on the walls of the lymphatic glands and are reproduced by direct division, and possess a smooth diaphanous outer membrane and a nodally thickened reticulated framework, with a more unstable material in the meshes.

The Pulsations (*pulso*, I beat) or rhythmical contractions of the Ventricle of the heart furnish by their number a reliable index to the activity of the circulation, and in certain species of Gastropods are visible through the base of the last whorl of the shell, and in some delicately shelled Pelecypods perceptible near the umbones.

The alternate contractions and relaxations of the heart are so persistent that they have been observed to continue for some time after its removal from the body of the animal and when completely drained of blood; according to Lister, the pulsations will recommence even twelve hours after excision if the organ be moistened with blood.

The activity of the circulation is, however, influenced by many

conditions; age, exercise and temperature, each contributing to control its actions, while other less direct influences exert a subsidiary modifying effect.

Injuries to the shell or to the animal have also a disturbing effect upon the activity of the heart, whose pulsations are greatly accelerated even by the careful removal of a piece of the shell, so that any attempt to ascertain the pulse rate in the thick-shelled species, by removing, however carefully, the shell covering the cardiac region, would only yield misleading results.

Age, as in other animals, has a great influence on the rapidity of the heart's pulsations. In man, according to Carpenter, the pulse decreases in rapidity from about 135 at birth to 85 in youth and 72 in adult life, and in the mollusca there is the same change from the rapidly pulsating heart of the embryo to the comparatively deliberate contractions of the mature animal; this being confirmed by Stiebel, who has recorded that in the embryo of *Limnæa* there are from 50 to 70 pulsations per minute, which decrease to 30 as the animal advances in growth and eventually sink to 20 at maturity. The retarding influence of age is readily verified by comparing the rate of pulsations in immature and adult specimens of the same species under similar conditions; thus an immature *Helix cantiana* showed 56 pulsations per minute, and a mature specimen of the same species 44 only; a young *Helix hortensis* showed 74 per minute, while a full-grown individual was only 58 per minute.

Exercise has also, as in man and other animals, a most striking effect on the heart, varying according to the amount of exertion and other circumstances, the mere act of emerging from the shell almost instantly accelerating the pulse rate. A *Hyaliuia cellaria*, whose heart in repose beat 40 times per minute, immediately increased to 64 on the emergence of the animal from its shell; *Helix hortensis* under similar circumstances showed a similar rapid augmentation from 58 to 80, the acceleration in all cases being more abrupt at the muscular effort to commence movement than at the effort necessary to continue it, thus the pulsations of a quiescent *Helix granulata* rose abruptly at the earliest movement from 46 to 54 per minute, afterwards gradually increasing to 58, 60 and 64 as the animal extended itself.

Temperature is of pre-eminent importance in influencing the action of the heart, although its effects have been overlooked by

most writers on malacological subjects, who have been usually content to cite the bare numerical result of a single observation, without noting the conditions affecting the rapidity of the pulsations.

Moquin-Tandon, in his admirable work on the Mollusca of France, records that the heart of *Vitrina pyrenaica* beats 44 times per minute and states that St. Simon had noted 85 pulsations in *Helix fusca*, leading to the erroneous conclusion that the circulation of *Helix* is normally twice as active as that of *Vitrina*. Mr. Alder has also recorded that he counted 120 pulsations per minute in *Vitrina pellucida*, and this observation also conveys a wrong impression, as to observe so feverish a rate Mr. Alder probably held the shell between his fingers during examination, which also may have taken place in the sun or in a very warm room, as the heart of that species when resting in its usual haunts seldom exceeds 50 pulsations per minute, its optimum rate being probably between 30 and 40.

Moquin-Tandon has also recorded that the range of pulsations in Gastropods varies from 25 to 85 per minute, leading his readers to the wrong conclusion that the pulse never rises above the latter number nor falls below the lesser one.

The striking effect of warmth in stimulating the heart's action is readily seen by observing the pulsations of a suitable species in its cool natural retreat and again after it has laid a minute upon the

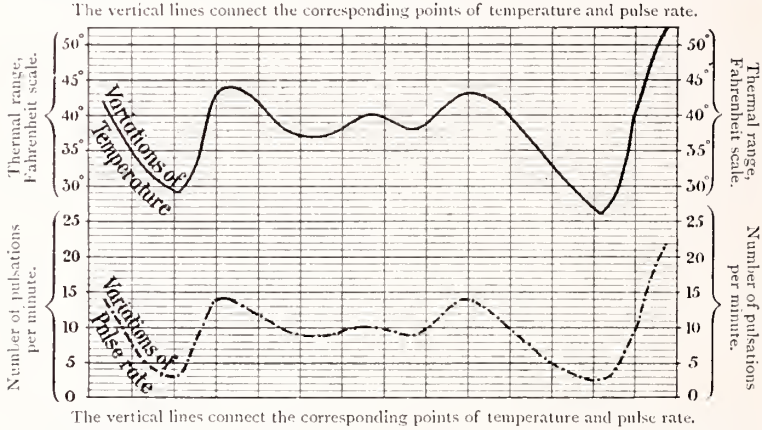


FIG. 588.—Diagram of the pulsations of the heart of *Helix hortensis*, especially illustrating the close correlation of its activity with the changes of temperature and showing the stimulating action of warmth and the inhibitory character of a decreasing temperature.

palm of the hand, when the rapid change from a deliberate to a quickly beating pulse will be plainly visible to the eye. *Vitrina pellucida*, under such circumstances, may increase its heart's pulsa-

tions from 50 to 98 beats per minute, and a young *Helix aspersa* from 70 to 110, while if the warmth be increased the heart's action seems to degenerate to a rapid and tremulous agitation, after which heat rigour probably soon supervenes.

Reductions of the temperature will similarly lower the pulse with equal rapidity, the pulsations becoming less and less numerous until, at a few degrees below freezing point, they may be reduced to 3 or 4 feeble contractions per minute. A *Hyalinia cellaria*, whose pulse whilst on the palm of the hand beat at the rate of 74 per minute, was exposed to the cool draught at a slightly open window and the pulse within two minutes fell to 26.

The heart, being so responsive to variations of temperature, quickening under the influence of noon-day warmth, and being retarded by the colder air at night, produces, in the rate of pulsations, a well-marked diurnal range, which more or less closely corresponds to the daily variations exhibited by the thermometer.

This susceptibility is indeed so delicate that even the play of the observer's warm breath during a short examination is sufficient to appreciably accelerate its rate of contraction; we should, therefore,

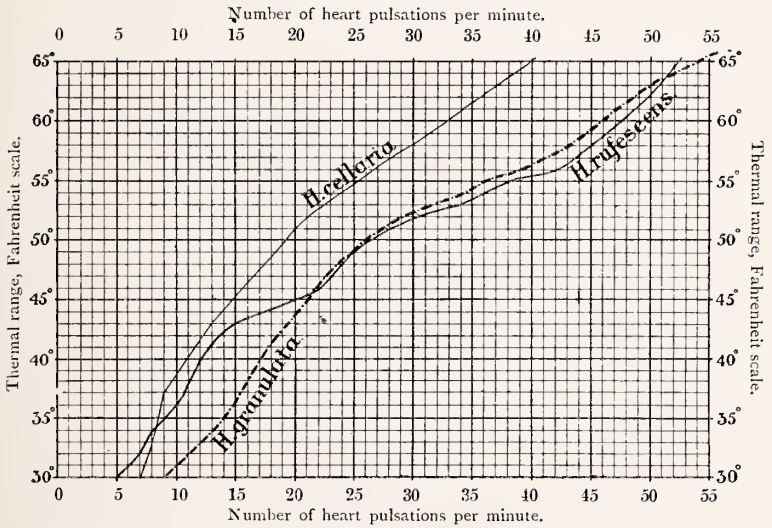

Number of heart pulsations per minute.
0 5 10 15 20 25 30 35 40 45 50 55
65° 60° 55° 50° 45° 40° 35° 30°
Thermal range, Fahrenheit scale.
H. cellaria
H. rufescens
H. granulata

FIG. 589.—Thermal-pulsatory curves of *Helix rufescens*, *Helix granulata* and *Hyalinia cellaria*, illustrating the effects of fluctuations of temperature as variously affecting the rapidity of the heart's pulsations in different species.

naturally expect to find an extremely rapid pulse in summer when the thermometer registers 80° or more, but, with few exceptions, our species do not voluntarily expose themselves to such heat, but retire

to cooler quarters among damp moss or herbage, etc., where, owing to evaporation, the temperature may be as much as 20° below that indicated by a neighbouring thermometer.

Every species and every individual, however, naturally seeks those conditions most agreeable to its own welfare, and it is probable that in correlation with this habit there is for every species a special optimum external temperature and also an optimum pulse-rate, especially suited to the action of its organs and to the requirements of its economy. Some species, like *Helix pisana* and *Helix cartusiana*, habitually expose themselves to the full glare of a burning sun and have probably a high optimum pulse-rate; others, which secrete themselves during the heat of the day in moderately dry and sheltered spots, attached to stems or undersides of leaves in hedgerows, have a pulse-rate varying between 35 and 60; while species which habitually hide themselves in wet moss or at the roots of damp herbage range between 25 and 45 per minute.

The Aquiferous or water-vascular system in the mollusca is most developed in the marine Pelecypods, some species possessing a complete network of ramifying canals within the foot, which, by the inception of water from without, render the foot turgid and firm, supplementary to the turgescence due to the retention of the blood therein.

Absorbent or minute pore canals opening to the exterior have also been affirmed to exist in our British Unionidæ and Sphæriidæ and are stated to have been observed even in *Helix pomatia* and other terrestrial species, the Limaces being specially noticeable for the rapid absorption of moisture by their integument.

Respiration is a process vital to animal existence, and in the lower forms of life may be accomplished simply by an interchange between the surface of the body and the surrounding medium, but in the more highly organized animals this interchange between the gases of the blood and tissues is chiefly performed by specialized and suitably placed organs, whose respirations or breathings, like the pulsations of the heart, vary in number in different species and also differ according to temperature, and the age, amount of exertion, etc., of the individual, but are always much more slowly and irregularly performed, the energy and activity of the organism being in proportion to the amount of oxygen absorbed.

The function of respiration is to supply oxygen to the blood and tissues and to eliminate the gaseous products of decay, and essentially consists in the exposure of the impure venous blood to the vivifying influence of air, or water containing air, so that oxygen is absorbed and carbonic acid eliminated.

This result in the mollusca is accomplished chiefly by branchiæ in the aquatic species and by a lung cavity in the terrestrial forms. Auxiliary to the respiration carried on in these specialized organs, there is cutaneous respiration and tissue or internal respiration.

Branchiæ (*βράνχια*, the gills of a fish) or Gills, the specialized organs for the respiration of water, are differentiations of the integument, and are in strict correlation with an aquatic life, and therefore of greater extent and complexity than the lung of the Pulmonates, to compensate for respiring a medium containing so little oxygen.

The Ctenidia (*κτενιδιον*, a little comb) or primitive molluscan gills are typically symmetrical and paired free plume-like structures, although it is only in some of the Pelecypods and Zygobranchiate Gastropods that their original character and arrangement are preserved.

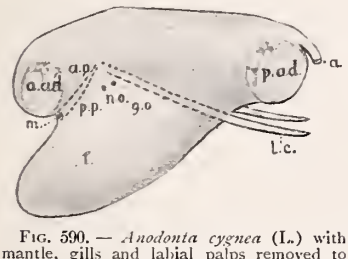


Fig. 590. — *Anodonta cygnea* (L.) with mantle, gills and labial palps removed to show the Lophophoral line (after Lankester).

a.a. line of attachment of the anterior palp and *p.p.* of the posterior palp, continuous with *l.c.* the line of attachment of the left ctenidium or gill, jointly forming the Lophophoral line ; *a.ad.* anterior adductor ; *p.ad.* posterior adductor ; *m.* mouth ; *f.* foot ; *n.o.* nephridial opening ; *g.o.* reproductive orifice.

They are assumed to have arisen as simple ridges at each side of the body, along a line extending from the mouth to the anus, known as the Lophophoral (*λόφος*, a plume ; *φόρέω*, to carry) line on account of its relation to the oral disk or lophophore of the Polyzoa, etc. These ridges, by elongation, each give rise to a row of hollow, ciliated respiratory processes, usually stiffened by chitinous rods, along one edge, each filament containing afferent and efferent axial vessels, and bearing at each side numerous delicate and perpendicular vascular processes, lined interiorly with connective tissue and supported by muscular trabeculæ, which under nervous influence, relax and contract, assisting to alternately receive and expel the blood. In the ancestors of most of the active Gastropoda the lateral gill-processes and the area occupied by them, from various causes, become more restricted and tend also to be relegated towards the rear of the animal.

In our Pelecypoda the branchial filaments have continued to elongate, and to secure freedom of growth have bent back upon themselves, so that the paired filaments on each side suspended from their point of support, which previously formed an inverted **V**, are, by the reflected growth, converted into a figure resembling the letter **W.**

The separate filaments may, however, combine together and form a plate-like, although perforate, gill, this fusion and vascular continuity of the constituent filaments being preceded by the close interlocking of the cilia clothing their surface and followed by a more or less intimate interlamellar concrescence. The primitive filamentous condition may, however, arise secondarily by the splitting up of previously existent lamellate gills, as is stated by Korschelt to be the case with *Sphærium*.

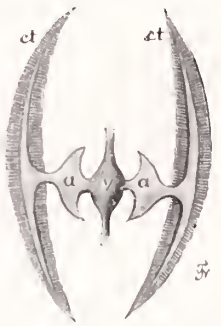


FIG. 591.—Ctenidia or gills of a Dioto-cardiate Pelecypod showing their paired bipinnate character (after Lang).

ct. ctenidia or gills, whose efferent ducts lead to the paired auricles, *a.a.*; and thence pass to the ventricle *v*.

The posterior mantle margin, in the burrowing species, is often produced into one or a pair of tubular processes or siphons for the purpose of conveying the water to and from the gills; the lowermost, known as the branchial or afferent siphon, is encircled by a number of long sensitive filaments or tentacula; the other, known as the anal or efferent aperture or siphon, carries away the respired water after it has passed over the branchiæ, and is usually shorter and more dorsally placed, with occasionally a filamentous termination.

In the marine burrowing species, the respiratory siphons are very long and very extensile, but usually correspond to the depth of the burrow occupied by the mollusk, although species like *Anodonta cygnea*, which possess comparatively rudimentary siphons, sometimes live buried beneath ten inches or more of soft mud and yet preserve free communication with the water above by means of vertical perforations through the soil, formed and kept open by the siphonal currents.

The Pelecypoda have been classified by Pelseneer into five groups, based upon the amount of specialization the gills have undergone, the simplest being known as Protobranchiata and the most specialized as Septibranchiata, these being connected by the groups Filibranchiata, Eulamellibranchiata and Pseudolamellibranchiata; all our British

species, however, are Eulamellibranchs, in which the filamentary processes have become fused together and form more or less complexly perforated and folded gill plates, lying in a branchial chamber; the interlamellar cavities, in some species, serving as marsupial or incubatory pouches for the protection of the eggs or young.

The delicate branchial tissue is easily detached in minute flakes by compression or friction, the detached fragments moving about like living Infusoria by the action of the cilia clothing their surface. Müller actually described these motile particles as species of his Infusorian genera, *Trichoda* and *Leucophra*.

In Gastropods the gills, though simpler in character, are constructed on the same plan as those of the Pelecypods and occupy a similar, though more restricted, position, but, owing to body torsion, the primitively left gill has become atrophied in all our species, although still present in a more or less primitive form in the Zygobranchiata. The gills are usually now of a semipinnate character with the axis fused to the roof of the mantle chamber, the respiratory processes being arranged parallel to each other, like the teeth of a comb, and freely projecting into the respired water.

FIG. 592.— Ctenidium or gill of a Monotocardiate Gastropod showing its pinnate character (after Lang).

ct. ctenidium or gill with efferent blood vessel leading to the auricle, *a.*; *v.* ventricle terminating in *a a.* anterior aorta and *p.a.* posterior aorta.

In the branchiate species respiration is probably more or less continuous when in process, more especially in the Pelecypoda, in which the alimentary function is so intimately combined with that

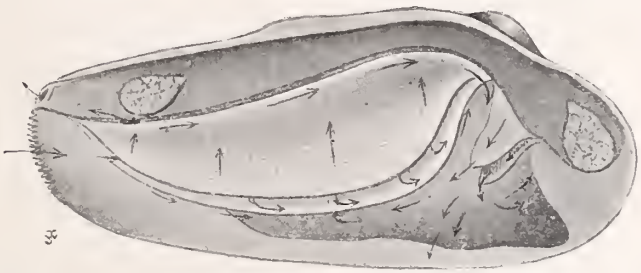


FIG. 593.—*Unio pictorum* (L.) with right valve and mantle removed to show the courses of the water currents during respiration (after Ölt).

The arrows indicate the courses traversed by the inspired water.

of respiration. The currents produced by the dense ciliary investment enter by the inhalent aperture, and are affirmed to flow in a steady and continuous stream along more or less definite and precise

tracks or courses, passing through or over the gills and leaving the body by the exhalent aperture.

Secondary Branchiæ are developed amongst our native species only in the *Limnæidæ*, a group which have relinquished terrestrial life to resume an aquatic one, and which are even now undergoing the process of re-adaptation to the respiration of water, this being shown by the diminution or loss of the pulmonary cavity and the increasing vascularity of the exsertile, tegumentary appendage bearing the anus and known as the Auriform lobe; this new organ of respiration is now actively functional in *Planorbis corneus* and other species. In the marine genera *Patella*, etc., this re-adaptation has taken the form of vascular outgrowths within the respiratory cavity, but the same result may be attained in other groups by different methods.

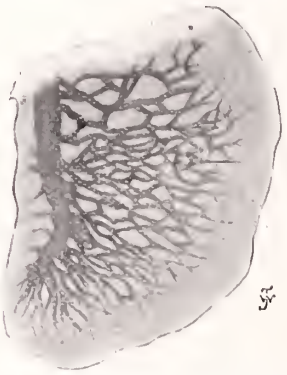


Fig. 594.—Auriform lobe or secondary branchia of *Planorbis corneus* (L.), × 12, showing its highly vascular character (after Pelseneer).

The Pulmonary Chamber of the Pulmonata is not morphologically a true lung, as in the Vertebrates, although physiologically performing similar functions. The vertebrate lung is a diverticulum of the alimentary canal, but that of the Pulmonates is really only a modification of the branchial cavity of the aquatic species, in which the

Fig. 595.—Roof of pulmonary cavity of *Limax flavus* (L.), seen from below × 3 (after Leidy), showing the relationship of the heart and the blood vessels of the lungs.

a. auricle of the heart receiving the oxygenated blood from the lung plexus; *v*. ventricle of the heart; *k*. kidney or renal organ; *u*. ureter; *r*. rectum; *e.o*. excretory orifice; *r.o*. respiratory orifice.

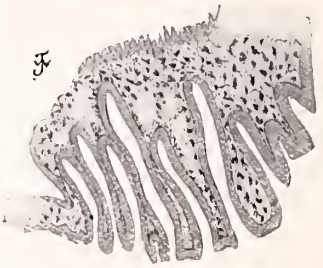


Fig. 596.— Longitudinal section through mantle of *Cyclostoma elegans* (Müll.), highly magnified, showing the folds of the vestigial branchia (after Garnault).

ctenidium or primitive gill has become atrophied and lost, and the anterior margin of the cavity has become fused with the dorsal integument, except at one point which constitutes the pulmonary aperture, where air is admitted and expelled for respiratory purposes, or, as in the aquatic Pulmonata, for hydrostatic purposes also. Upon the walls and more especially upon the roof of the respiratory cavity, a complex network of delicate blood vessels has been developed, a change necessitated by the adoption of terrestrial life and aerial respiration by the ancestors of the Pulmonata; although the Pulmonates are not a homogeneous group, but of polyphyletic origin, several distinct families having branched off in this direction. The pulmonary chamber has been aptly compared to a single air cell of the mammalian lung, as in both there is a cavity lined by a delicate vascular membrane supplied with impure venous blood, with air in contact with the free surface.

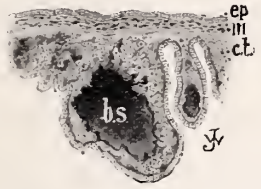


FIG. 597. — Blood sinus of lung wall of *Helix pomatia* L., highly magnified (after Vogt and Yung).

b.s. blood sinus; *ep.* epithelium; *m.* muscular layer beneath a stratum of connective tissue bearing pigment cells; *c.t.* connective tissue cells.

In terrestrial and fluviatile Pulmonates, although the breathing or opening and closing of the single pulmonary orifice is more actively rhythmical than in the branchiferous species, yet there is not the same methodical and regular isochronous succession of respiratory movements as previously described in the movements of the heart.

SCALE :—30 mill. = one hour.

FIG. 598.—Diagram illustrating the respiratory action at 65° F. of a specimen of *Planorbis corneus* (L.), from Wansford, near Beverley.

The times mentioned on the diagram represent the number of seconds the respiratory orifice remained open to the air at each inspiration, their duration being too brief to allow of indication according to scale. The horizontal line below the level of the surface of the water is to scale and represents the time the animal remained beneath the surface between the respiratory acts.

The renewal of the air within the pulmonary cavity takes place when the respiratory aperture is opened, and is chiefly accomplished by diffusion; exactly as when a door is opened to ventilate a room, the incoming purer air being stated to follow a certain well-defined course within the lung-cavity, and to gradually replace that which has become effete by respiration; the process being, however, assisted by the contractions and relaxations of the muscular walls of the cavity.

Thermal conditions also variously affect or influence the activity of the respiratory function in different species, some species being more susceptible and responsive to the fluctuations of temperature than

FIG. 599.—*Limax maximus* L., with shield removed, to show the course traversed by the respiratory air current (after Dr. T. Williams).

The arrows show the general direction affirmed to be followed by the pure air at each inspiration.

others. The fluviatile Pulmonates do not, however, exclusively respire air, but may at times be observed to regularly open and close their respiratory orifice when beneath the surface, more especially when the inhabited water departs from a medium temperature.

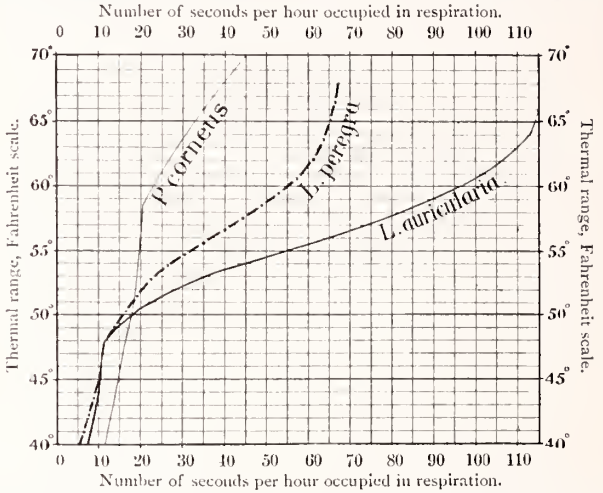

Number of seconds per hour occupied in respiration.
0 10 20 30 40 50 60 70 80 90 100 110
70° 65° 60° 55° 50° 45° 40°
Thermal range, Fahrenheit scale.
P. cornens
L. peregra
L. auricularia
Number of seconds per hour occupied in respiration.

FIG. 600.—Thermal-respiratory curves of *Limnæa peregra*, *Limnæa auricularia* and *Planorbis corneus*, illustrating the varying degree in which changes of temperature affect the rapidity of respiration in different species.

NOTE.—The results indicated in the above diagram of the action of the respiratory organs show the average results of a large number of observations upon individuals kept in confinement, and it is possible that a more extended study under less artificial conditions will modify to some extent the results attained, as it may eliminate any effects due to abnormality in the mollusks themselves or their surroundings.

CUTANEOUS RESPIRATION is actively carried on through the general integument, especially by the slugs and other genera, and though usually subsidiary to that of the gills or lungs, yet, in some forms, as *Anodonta*, etc., the surface of the mantle may perform the function of respiration even more effectually than the gills.

Cutaneous respiration in the Pulmonate species may, under certain conditions, be the chief mode of respiration, and practically constitute

the whole respiratory function, as in the cold abyssal depths of the Lake of Geneva, where several minute species of *Limnæa* permanently dwell, their pulmonary sacs filled with water, and aquatic respiration taking place by the lung cavity and by the integument, a prolongation of the aqueous respiration of the embryo and newly-hatched young of the aquatic Pulmonates.

During winter, when the pools are frozen and access to the air cut off, various species of *Limnæidæ* may often be observed beneath the ice crawling actively about and probably mainly respiring by their skin.

Respiration by the skin is assisted by the presence therein of superficially placed coloring matters with an affinity for oxygen, as exemplified in the orange-coloured foot of many Pelecypods, this colouring being usually due to Tetronerythrin, a substance combining readily with oxygen. The integument of *Limax flavus*, etc., has also yielded pigments which, in addition to other duties, are also functionally respiratory.

TISSUE RESPIRATION is greatly developed in mollusca and is chiefly performed by means of the varied pigments so plentiful in the molluscan organism, and although their chief function is doubtless respiratory, as they combine with and retain oxygen within the system, yet they have also other functions, as in perfecting protective resemblances or acting as screens to underlying cells.

These pigments, known as Enterochlorophylls and Enterohæmatins, were first discovered by Dr. Sorby, and apparently contribute to replace hæmoglobin in the Invertebrate system.

The ENTEROCHLOROPHYLLS (ἔντερον, gut ; χλωρός, green ; φύλλον, a leaf) found in the digestive gland are identical with the hepatochromates, and occur dissolved in oil globules and in the protoplasm of the secreting cells, though also found in a granular form. They are probably formed by the action of the digestive fluids upon the chlorophyll of the food, and eventually become lodged within the digestive gland and other organs.

The ENTEROHÆMATINS (ἔντερον, gut ; αἷμα, blood) also occur chiefly in the digestive gland, though present in various other parts of the body. MYOHÆMATIN (μυς, muscle ; αἷμα, blood) is the true intrinsic coloring matter of invertebrate muscle, while HISTOHÆMATIN (ἱστός, tissue ; αἷμα, blood) is characteristic of organs and tissues, but both may be reinforced or replaced by hæmoglobin where extra activity of internal respiration is required.

Probably all these substances are formed on the same basis, as hæmatoporphyrin is yielded on decomposition by all of them.

The TEMPERATURE of warm-blooded animals is maintained at a nearly uniform standard under all changes of external temperature by combustive processes within the body, but in the mollusca and other cold-blooded animals, owing to their sluggish respiration, the oxygenation is so feeble that very little heat is generated and the bodily temperature fluctuates with that of the inhabited medium.

Repeated observations have established that the temperature of land snails practically accords with that of the atmosphere if it be moist, but in dry weather the heat of the animals may be reduced below that of the air, probably by the increased evaporation from the body of its natural moisture.

Although a single *Helix* or *Limax* confined within a limited space causes no perceptible thermometric change, yet if several be enclosed together the temperature has been noted by different observers to rise from 0·24° to 3·90°.

The Pelecypoda likewise maintain a temperature similarly in accord with that of the water they inhabit, varying in the *Anodontæ*, according to different observers, from 1·0° colder to 0·30° warmer than the respired water.

ÆSTIVATION (*æstivo*, to pass the summer) is the period of torpidity undergone during the prevalence of dry, hot, summery weather, and though, in this country, this state is essentially transient and short, yet in warmer regions this torpor persists for lengthened periods, embracing the entire dry season, the land mollusks constructing a more or less filmy and delicate epiphragm (see p. 129) and burying themselves more or less deeply in the ground or attaching themselves by a viscous secretion in some suitable position. Many freshwater species also bury themselves deeply in the soft mud when the waters they inhabit are becoming dried up.

Hot dry weather is especially fatal to slugs, which therefore burrow into the earth and enclose themselves within a coating of mucus, which on drying prevents further evaporation. The figurative and beautifully expressive simile of the fate of the ungodly given in our Prayer Books, "Consume away like a snail," aptly illustrates their inability to withstand heat or dryness.

The forms most subject to seasonal torpidity are naturally those most remarkable for their tenacity of life, some species being known

to survive after more than five years' abstinence from food; even our *Helix nemoralis* has been recorded as having endured more than three years' starvation, and many other striking examples of this faculty are known.

Hibernation (*hiberno*, to spend the winter), or winter torpor, is induced in the mollusca and other organisms by the advent of cold, and is obviously related to sleep, of which it seems but an intensification, enabling the mollusk to successfully resist the extreme reduction of temperature and the absence of accustomed food.

At the approach of winter and in the more sensitive species often as early as October, the mollusks, being then plumper and better nourished than at other times, gradually become less voracious and more sluggish and lethargic, the terrestrial species retiring to their accustomed or temporary places of shelter, frequently clustering together in the crevices of walls, rocks, and trees, or ensconcing themselves deeply amongst dead leaves or in the earth, in which latter case the mouth of the shell is invariably directed upwards and often level with the surface of the soil, the epiphragm or cover to the mouth of the shell (see p. 130) being then secreted, to protect the animal from the weather and other dangers and to prevent the evaporation of its natural moisture, the activity of their respiration also diminishing as the temperature becomes lower and lower, until the animals fall into a hibernal sleep or die.

This comatose state may be partial or complete according to the age of the animal, the hardihood of the species and the character of the winter, whether it be continuously severe or present comparatively mild intervals; as during such intervals, if sufficiently mild, the winter sleep, especially of the more immature individuals, may be broken and the mollusk wander about in search of food.

In a hard winter the animal contracts more and more closely within the spire of the shell, forming any additional epiphragms necessitated by the smaller compass into which the mollusk has compressed itself; the young individuals are, however, less susceptible to cold than mature animals, retiring later into winter quarters and re-appearing earlier and perhaps only becoming really torpid during the continuance of actual frost, this superior hardihood of the younger animals being possibly due to their more active circulation.

Many of the fluviatile species during severe weather bury themselves in the mud of the ponds or rivers they inhabit, and even

Dreissensia casts off its byssus and also retires beneath the bottom mud, as its temperature is always higher than that of the superimposed water.

The amount of cold mollusks can endure is, however, not unlimited, as Moquin-Tandon records that Helices, though capable of enduring 16° Fahr., freeze at 14° Fahr., and the endurance of this great cold implies the possession of internal heat sufficient to counteract the reduction of temperature, perhaps partially due to the excess of respiratory pigments present in the tissues in winter.

Hibernacula (*hibernaculum*, a winter abode) or winter shelters may be more or less adventitious or may be places of more regular resort utilized by the mollusks, not only during their seasons of protracted torpidity, whether arising from cold or dryness, but as places of safety during their diurnal siesta.

In certain districts the carboniferous limestone rocks are almost honeycombed by tubular excavations, which, though probably made and chiefly tenanted by *Helix aspersa*, are occasionally occupied by other species, not only to pass through the periods of hibernation and æstivation, but as regular resorts for rest and shelter.

These galleries, which almost invariably take an upward direction, perpendicular to the bedding of the strata, rarely occur on rocks approaching grit or on rock-faces exposed to the prevailing winds, but are usually clustered beneath projecting rock-ledges or pierced in the face of those cliffs facing east or north-east, being thus protected from the wet west and south-west winds. When placed upon the face of a vertical cliff the burrows may originate as a slight channel and sink gradually into the rock; frequently, however, they originate beneath a slight prominence, as though the snails had formerly sheltered there and gradually worked their way into the stone.

These rock tunnels are generally about one inch in diameter and sometimes three inches or more in depth, smooth and regularly shaped inside, but often containing subsidiary depressions upon their walls, due to a persistent use of those particular spots as resting places by many snails; they must not, however, be confused with the oval or circular cavities due to weathering nor with the bitterspar concavities so common in the magnesian limestone, whose walls are often encrusted with crystals of lime, as such natural cavities frequently are.

These tunnels were formerly surmised to be the work of the Pholades or other marine boring mollusks, during the period the rocks were

submerged in the ocean, and that upon their upheaval the Gastropods now occupying these burrows merely appropriated them as convenient places of shelter, but that the snails have themselves formed these rock-tunnels may, however, be almost confidently assumed, not only because Helices, especially *Helix aspersa*, are generally abundant near the burrows and that living specimens are always found in the

Fig. 601.—Hibernacula or Rock-burrows formed by *Helix aspersa* Müll., discovered in the Great Ormes Head, North Wales, by Mr. R. D. Darbishire, B.A. (modified after Prof. Bonney).

The vertical cliff had a north aspect; the small detached fragment at base, though from a south aspect formed the roof of a horizontal fissure.

freshest and least weathered tunnels, but also from their characteristic *ascending* direction with the opening below, which clearly distinguishes these Helicidian cavities from those of the marine boring mollusks, which usually follow a *descending* direction with the mouth of the tunnel opening above.

The ability of the Helices, in course of ages, to excavate these tunnels can scarcely be questioned, as, in addition to their demonstrated power to abrade limestone and chalk with their odontophores, M. Bouchard-Chantereux has affirmed from actual experiment that their mucoid secretions exhibited a distinctly acid reaction, testified by the reddening of litmus paper, and would, therefore, tend to dissolve the rock and thus facilitate the process of the excavation. Probably, however, the movements of the snails within the cavities have been a chief cause of their excavation, the wearing power of the friction of the foot being clearly demonstrated by the worn margins of the cavities, and by the sunken tracks leading thereto, worn away in the rocks by the passage to and fro of the countless generations of snails which have for untold ages sought their shelter.

These rock galleries or other permanent shelters, regularly resorted to by snails as resting places after their crepuscular or nocturnal rambles, imply the possession of a sense of direction, or what may be termed orientation, in those species possessing regular abodes; this perception or recognition of locality may be due to the delicacy of their olfactory sense, and has been distinguished as the faculty of homing.

This Homing power has been especially observed in *Helix aspersa*, though several other of our terrestrial species have been undeniably demonstrated to also possess settled places of abode or homes to which they regularly return, yet there are doubtless many others which have no settled habitation, but conceal themselves alone or in company beneath any suitable shelter which may happen to be convenient to their food.

The inter-tidal peregrinations of the marine limpet and its unfailing return to the precise spot upon which it is in the habit of resting, first attracted attention to this subject, and it has been demonstrated that their track when carefully followed almost invariably describes a double loop which may be likened to a variably proportioned figure of 8, and though this peculiarity is not shared by every species, yet the path, followed by some of our terrestrial homing snails, during their foraging expeditions, have been observed to exhibit or describe the same remarkable figure.

Helix aspersa is particularly noticeable for its love of home and for the exertions it will make to regain its shelter, having been observed to traverse with great labour broad dusty roads or climb

rough walls to reach some favourite food, and when satiated not retiring at daybreak to the shelter of any convenient crevice, as might be supposed, but almost invariably retracing its often toilsome and arduous way to reach its favourite shelter, a peculiarity that has been verified by many observers on numerous occasions.

The complex tracks formed by the nocturnal foraging expeditions of *Limax maximus*, *L. flavus*, and probably other species, which are sometimes so readily traced by the mucous trails they leave behind, also very frequently describe the double-loop or figure of 8 already mentioned, as distinguishing the track of *Patella vulgata*.

FIG. 602.—Mucous track of *Limax flavus* L., 19 feet in length, as observed by Mr. H. Wallis Kew, F.Z.S., on a flagged garden path at Louth, Lincolnshire.

Mr. Lionel E. Adams at my request kindly made many careful diagrams of limacidian tracks at Ashbourne, Derbyshire, and these almost invariably formed the same peculiar figure. The animals on setting out are probably guided by the olfactory sense as to the course pursued, but make a wide sweep upon the return home, and usually, though not invariably, cross the outward track at some point before again reaching the desired haven.

The GLANDULAR system is a well-developed and specially characteristic feature of the molluscan organism.

A gland is constituted by a collection or aggregation of simple secretory cellules which separate or elaborate from the blood certain products, which may be utilized in physiological processes or, if noxious, can be speedily expelled from the body.

The glands discharging externally are chiefly mucous, byssal, pigment and calcic glands, while the internal glands yield various products essential in the processes of digestion, reproduction and other phases of animal economy.

The chief mucous glands are the Ventral and Supra-pedal glands, the Caudal gland and the Hypo-branchial gland, but, in addition to these more important organs, there are

The Dermal Cells which are scattered plentifully over all the external surface of the body not covered by the shell, and abundantly secrete a fluid mucus, which is clear and transparent in many species, but tinged in others with pigment or may be obscured and rendered

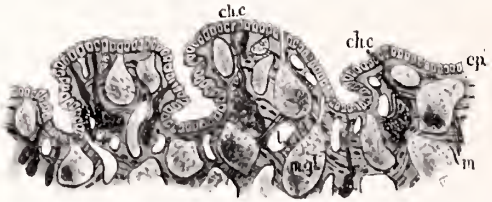


Fig. 603.—Section through a rugose glandular area of the back of *Helix pomatia* L., showing the scattered mucous and other cells, highly magnified (after Vogt and Yung).

ch.c. lime cells filled with granular substance ; *ep.* epithelium ; *m.gl.* mucous cells, some showing nuclei ; *l.* lacunæ ; *m.* muscular fibres to skin.

somewhat opaque by lime, which preserves the integument in a cool, moist and supple condition, a state vitally essential to their very existence, desiccation of the skin being quickly fatal. This dermal mucous secretion, especially of slugs, is also in some degree protective, evidenced by the manifest distaste of its adhesive character shown by some of their enemies.

The Anterior or Supra-Pedal Gland, known also as the Sinus of Kleebnrg and formerly considered as having an olfactory function, is a very important organ in the Gastropods, as it supplies the lubri-

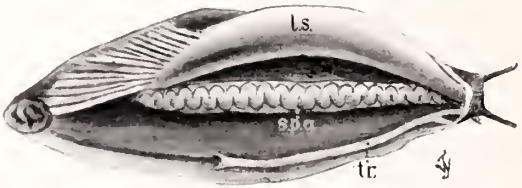


Fig. 604.—*Testacella haliotidea* Drap., × 2, laid open, the lingual sheath, with its powerful retractor muscles, turned outwards and the remaining viscera removed to show the position and general character of the Supra-Pedal Gland.

l.s. lingual sheath ; *t.r.* tentacular retractor of right side ; *sp.g.* supra-pedal gland.

cant mucus for smoothing the path to be traversed by the animal and also assists to ensure the necessary adhesion to the objects upon or over which it may crawl.

The gland is composed of large and oval nucleated secretory cells, with pale finely granular contents, which lie in the surrounding tissue and open on its walls, and is usually a vertically compressed and conspicuously folded canal strongly ciliated on its ventral surface and often quite as long as the foot itself, occupying the median line of the body above the sole, and partially embedded amongst the pedal muscles, but sometimes lying quite free within the body cavity, it serves as a reservoir and duct for the mucus issuing from the innumerable intercellular passages leading to it.

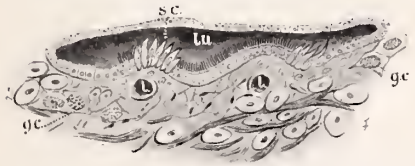


FIG. 605.—Transverse section through the pedal gland of *Limax maximus* L., highly magnified.
lu. lumen or cavity of gland ; *s.c.* nerve cells ; *g.c.* ganglion cells ; *l.* lacunæ.

The external aperture of the gland is between the mouth and the anterior end of the foot, the mucus being driven out by the action of the cilia, by muscular compression of the cavity, by the undulatory action of the foot during locomotion, and by the general movements of the whole body, and forming the glistening iridescent tracks which so distinctly mark the path travelled by the mollusk (see p. 313, f. 602, and which are not only perceptible on land, but in the stiller pools these slime-tracks are left on the surface of the water by the larger *Limnæa*, and may at times be observed of considerable length.

FIG. 606. — Portion of pedal gland of *Testacella haliotidea* Drap., highly magnified (after Lacaze-Duthiers), showing its convoluted character and the investing tissue.

The numerous mucous tracks of *Limnæa stagnalis* observed by Mr. Henry Crowther upon the surface of Tag Lock, near Elland, Yorkshire, on a warm still day in August, 1898, were several yards in length, crossing and recrossing each other many times.

Slime-tracks do not, however, actually possess the glassy smoothness of surface they apparently present to a cursory observer, but are really composed of a multitude of transverse wavy ridges, about a millimetre apart with intervening depressions, this appearance being evidently a reflection and effect of the undulatory movements of the foot-sole.

The VENTRAL GLAND present in *Cyclostoma* and other Streptoneura, as well as in the *Limnæidæ*, is a ramified cavity within the foot,

within which is accumulated the viscid mucus secreted by the follicular tissue by which it is densely invested. The gland opens upon the lower surface of the foot towards its anterior end and corresponds to or is probably homologous with the byssal gland of the Pelecypoda, secreting a viscid and very tenacious mucus by means of which firm adhesion can be secured to their resting place, or a strong filament can be formed for suspension or descent from an elevated position.

Fig. 607. — Mucous track on surface of water formed by *Limnæa auricularia* (L.) in the aquarium.

The Mucous Filaments formed by the attenuation of the viscid and tenacious slime emitted from the foot glands, which, by its property of hardening when in contact with air or water, supplies the mollusca with a ready means of locomotion or suspension from suitable elevated objects or from the surface of the water, have been specially studied by Mr. G. Sherriff Tye, who has added greatly to our knowledge of this subject.

The British Isles, owing to their cool and damp climate, are especially favourable countries for the observation of this curious and interesting habit amongst our land mollusca, the slugs possessing this power in the most marked degree, *Limax marginatus* Müll. olim *Limax arborum* Bouch.-Ch. performing these actions with especial ease and celerity, though other species under similar circumstances form these suspensory filaments with great facility, lowering themselves from a branch or other elevated object to a lower level by attaching the viscid mucus accumulated at the tail to the branch or other object upon which the animal may happen to be and then by launching into the air, attenuating and lengthening out into a slender thread-like filament the accumulated mucus, a fresh supply for its increasing length being afforded by its continued free exudation from the foot-glands, which is carried towards the tail by the active undulatory motion of the sole or locomotory disc, the sides of the foot being brought nearer together and forming a guide or

groove leading to the origin of the suspensory filament, and although the mucus may become too thin to safely sustain the weight of the creature when gorged to repletion, yet when in need of food the mucus is more tenacious and becomes available as a ready means of transportation from one level to another.

FIG. 608. FIG. 609.

FIG. 608.—*Arion hortensis* Fér. descending by the aid of a slime thread.

FIG. 609.—*Arion subfuscus* Drap., young, re-ascending by means of a slime thread, which it had previously descended.

(Modified from original sketches by Mr. H. Wallis Kew, F.Z.S.)

It is, however, principally by the immature animals that this method of locomotion is indulged in, as when full size and weight is attained this method of progression is not so essential and becomes more precarious and uncertain.

The same mucous filament can also be made use of, if necessary, to re-ascend to the point of suspension, this being accomplished by bring-

ing the extremities of the body together and transferring the point of attachment of the suspensory filament from the tail to the head, the filament re-traversed in ascending being accumulated as an irregular mucous mass near the tail. The mucous filament has been ascertained by Mr. T. Hoy to be produced by *Limax flavus*, a variety of *Agriolimax agrestis*, at the rate of one-third of an inch per minute, while in regard to its possible length Mr. H. Crowther, in August, 1890, at Truro, observed a specimen of the same species in the act of descending from the branch of an elm tree twelve feet from the ground, the slug when observed having already descended seven feet of this distance.

Some Limaces have also been observed to use this power of producing mucous threads during sexual congress, spirally coiling around each other's bodies and suspending themselves heads downwards during that function by means of a jointly produced mucus cable.

The fluviatile mollusks, owing to the greater density of water, are, however, the greatest adepts at this mode of travelling, the Physinæ, and especially *Aplecta hypnorum*, making free use of this interesting mode of progression, and readily forming upwardly or downwardly directed mucous threads of considerable length, affixing them between different points where they may remain in position for a length of time and become thickened and strengthened each time of usage by the adhesion of the film of mucus left behind by each snail using the filament.

Fig. 610.—Suspensory mucous filament affixed to water surface and formed by *Limnæa auricularia* (L.) in the aquarium.

These filaments, when fixed, offer a convenient and direct means of access to the surface for respiratory purposes or permit an easy descent into the depths when the lung cavity is inflated with air and the animal and its shell thus rendered lighter than the water, into which it can only enter by expelling a portion of the air contained in the lung-sac or by crawling down a fixed filament, the stem of a plant or other suitable object.

Upward threads can only be formed by the aquatic Pulmonates, as being attached to some submerged object and always directed towards the surface of the water, they can only be formed by individuals using their air-inflated lung-sac as a hydrostatic organ enabling them to rise to the surface of the water, as they are then of less specific gravity than the water they inhabit.

Downward threads may be attached to the surface film of the water or to any object elevated above the surface of the mud, in the former case the exposed expanded face of the mucous filament being slightly depressed or hollow acts like a boat and supports the thread depending from it. The branchiate Streptoneura, especially when young, can form the downward threads, *Bythinia tentaculata* being observed to be particularly addicted to suspending itself from the surface of the water by this means. These filaments can also be formed by Pulmonates, which have expelled some of the air from the respiratory chamber and thus become heavier than the water they inhabit and tend to fall to the bottom.

The formation of mucous cords is not, however, confined to the Gastropods, as they are also made use of by certain of the Pelecypoda, especially when young, *Sphærium lacustre* being especially noted for indulging in this habit of suspending itself, sometimes for hours, from the vegetation or the surface of the water, by one or more mucous threads; the rate of production of these filaments being recorded as three hours for the formation of a filament half-an-inch in length.

The Caudal Gland is usually constituted by an actively secretory area, and a more or less triangular receptacle or cavity upon the upper surface of the extremity of the tail, and is present in a variously developed form in many diverse genera, but is especially conspicuous in the members of the genus *Arion*.

In *Arion* the glandular portion is formed by an aggregation of minute brownish, semi-transparent and rounded secretory cellules, which combine to form long, irregularly sinuate lobes, separable by maceration, the gland secretes considerable quantities of rather clear and tenacious mucus with great rapidity, especially during the pairing season, when large and conspicuous globules of glutinous mucus frequently accumulate within the caudal cavity or receptacle.

The Hypobranchial Gland is a localized and variously shaped mucous gland, intersected by nerves and blood vessels, and serving for the lubrication of the respiratory cavity and the organs therein.

In the branchiate species it is found as a more or less distinctly localized organ, with projecting folds or leaflets augmenting its secretory surface, and is placed between the rectum and the branchia on the roof of the respiratory cavity, the gland being capable, on occasion, of pouring out an enormous quantity of mucus which escapes through the respiratory orifice.

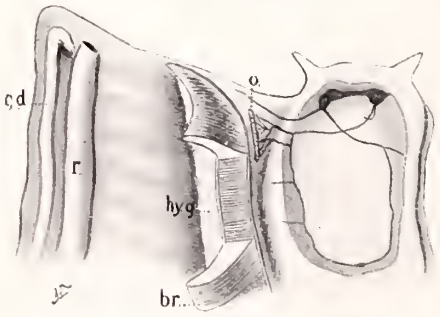


Fig. 611.—Dissection of *Viviparus vivipara* (L.) (after Bernard), greatly enlarged, showing the position of the Hypobranchial gland within the respiratory cavity, and incidentally the arrangement of other pallial organs and the innervation of the osphradium.

br. branchia, with leaflets partially removed; *g.d.* genital duct; *hy.g.* hypobranchial gland; *o.* osphradium; *r.* rectum.

In the Pulmonates the gland is not distinctly localized and the epithelial glandular cellules are distributed over the walls of the respiratory cavity.

The celebrated Imperial or Tyrian purple of the ancients was a product of the hypobranchial gland of species of *Murex*, heaps of whose broken shells may still be seen upon the Tyrian shores. The secretion, though colourless when discharged from the gland, becomes more or less brilliantly coloured in correlation with the intensity of the light to which it is subjected, passing through an intermediate and definite series of colour changes and emitting an unpleasant odour during the process.

Fig. 612.—Transverse highly magnified section through the Hypobranchial gland or mucous rib of *Viviparus vivipara* (L.) (after Bernard), showing its character and close relationship to the branchia and the subjacent blood sinus.

br. branchial filament in section, showing venous connection with *b.s.* blood sinus; *m.g.* hypobranchial gland or mucous rib.

The Byssal Gland, though the homologue of the ventral gland of the Gastropoda, is yet a characteristic peculiarity of the more sedentary Pelecypods, enabling them to securely maintain possession of any suitable station they may have selected as a permanent abode.

The byssal gland opens upon the median line of the hinder surface of the foot and consists of a byssal cavity with longitudinally plaited walls and numerous divergent ramifying channels, from which emanate the chitinous fluid which is secreted partially by their epithial walls and partly by the glandular cells imbedded in the tissues, whose

secretions permeate between the epithelial cellules and accumulate within the byssal cavity, flowing therefrom by a duct into a semilunar groove or furrow invested by large mucus cells which runs along the ventral edge of the foot and is capable of being converted into a closed canal, wherein the chitinous secretion is moulded into threads or filaments, which harden quickly on exposure, their adherent punctiform distal extremities being formed within a cup-like depression at the anterior end of the byssal furrow, within which is secreted the adhesive substance by the aid of which attachment is made.

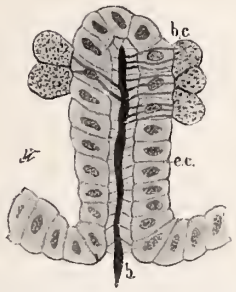


FIG. 613.—Transverse section of a furrow of the byssogenous cavity of *Modiolaria discors*, × 250 (after Cattie), showing the byssal filament and the formative secretion passing from the byssogenous cells between the epithelial cells to the byssal furrow.

b. byssal filament ; *b.c.* byssogenous cells, their secretion flowing between the epithelial cellules, *e.c.*

The byssus is composed of a bundle of tough chitinous fibres, resembling horn in some of its physical characteristics, but adhesive when first formed and therefore available as a means of anchorage to foreign objects. It can, however, if necessary be thrown bodily off and replaced by a new one when the animal desires to change its position, or the mollusk can ascend any smooth vertical surface by alternately fixing and rejecting a series of successively secreted byssal attachments, the rejected byssal tufts of *Dreissensia* being regarded by Dr. Mörch as constituting the *Tubularia caspia* of Pallas.

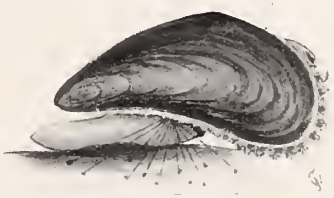


FIG. 614.—*Mytilus edulis* with extended foot in process of attaching a byssal filament (after Meyer and Möbius),

This gland when highly developed, as in *Dreissensia*, exercises a prejudicial influence upon the development of the foot itself, which may cease to be functional as an efficient locomotory organ, and diminish in size in inverse ratio to the development of the byssus, for which it comes eventually to serve merely as a support, the posterior pedal retractor muscles even becoming fixed to the gland and functioning as byssal retractors.

In the *Unionidæ*, *Sphæriidæ*, etc., the organ is more or less vestigial in the adult, though present and functional in the young. In

Anodonta, the larval byssal organ is a prominent and transparent tube, arising from the left side of the visceral mass and coiled around the adductor muscle, but opening on the median line of the body and emitting one or two long filaments, which, besides serving to anchor the embryos within the brood pouch, also tend to keep the glochidia together by their entanglement.

FIG. 615.— Larva or Glochidium of *Anodonta cygnea* (L.), greatly enlarged (modified after Balfour).

sh. shell, showing porous structure; *ad.* adductor; *bys.* byssus; *s.s.* sensory setæ; *m.* retractor muscle of apex of shell.

The byssal threads of *Pinna*, an exotic marine genus, are so long and delicate, and possess such a beautiful silky lustre that, according to Ogilvie, they are woven by the Italians into a valuable fabric, a manufacture known also to the ancients; *Modiola* utilizes its byssal filaments to form a nest or retreat, strengthening the walls by attaching extraneous matters thereto; while the shelly plug of *Anomia*, by which it is fixed to the ground, must also be regarded as a modified byssal attachment.

Some exotic marine species, as *Trigonia*, which, when adult, possess neither byssus nor byssal gland, have retained the byssal cavity, the duct and even the retractors; the abortion of the byssus is generally correlated with an increase in the size of the foot and with increased activity in the animal.

The CONCHAL or SHELL GLAND originates during the Trochosphere stage of larval life, as an invagination of the thickened centro-dorsal area of the body of the embryo; it secretes a viscid chitinous substance which hardens on exposure and is assumed to vestigially represent a shell formerly possessed by the mollusca, but which has become lost and is replaced by the secondary shell they now possess. We may thus speak of a Primary, a Secondary and even, in some cases, a Tertiary shell in the mollusca, recognizing that each fleeting embryonal phase is necessarily incomplete and often discontinuous owing to a suppression in the embryo of their full development.

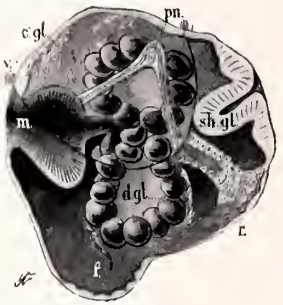


FIG. 616.—Embryo of *Limnæa stagnalis* (L.), approaching the Veliger stage, highly magnified, to illustrate the position and aspect of the conchal or shell gland (after Lankester).

sh.gl. shell gland; *m.* mouth; *r.* rectum; *d.gl.* developing digestive gland; *pn.* pronephros or larval kidney; *f.* foot; *v.* velum; *c.gl.* cerebral ganglion.

In some genera this transitorily developed primitive shell soon disappears and the shell-sac becomes everted, the thickened margins forming the collar of the mantle and with the enclosed area secreting the permanent shell.

Other groups, as *Limax*, *Clausilia*, *Vivipara*, *Neritina*, etc., however retain this embryonal vestige or Protoconch upon the apex of the permanent shell of later life. In the Limaces the invaginate gland closes up and the chitinous particle forms the nucleus of the permanent shell, which is secreted by the enclosing walls. In the *Clausilia* the minute vestigial shell is also enclosed and completely invested by the epithelium, which, however, is soon ruptured and the protoconch becomes partially external, the permanent shell being formed in continuity with it.

In the Pelecypoda a primitive shell, the Protostracum, is also developed early in embryonal life, and is followed by a Prodissoconch stage, the vestiges of which are frequently observed upon the umbones of immature shells. The conchal gland appears opposite the blastopore or orifice of embryonal invagination, as a saddle-shaped group of epithelial cells, secreting a uniform saddle-shaped film, which later becomes calcified laterally to form the paired valves, the uncalcified median part of the pellicle uniting the valves is placed over the median groove and becomes the ligament.

The Calcic Glands (*calx*, lime) are numerously distributed over the whole mantle-surface, but most richly developed along the mantle-margin in the shell-bearing species, and contributing to form the shell. Lime cells are also numerous in the digestive gland, their product being affirmed to be eventually largely utilized by the Gastropods in the production of the calcareous epiphragm; they are also distributed over the whole external surface of the body, especially in those species destitute of definite shells, calcareous granules or spicula being deposited in the skin, and probably contributing to the future development of a new shelly covering or protection for the body, to replace that now practically lost by degeneration, and constituting a renewal of the cycle of development of an external shell, such as has taken place more than once in the past, as evidenced by the transitory vestiges present temporarily in the early larval stages of many species and therefore preceding the shell they now possess.

Lime cells are also freely distributed throughout the general tissues of the body, their action under suitable conditions producing

separate or attached calcareous concretions, which are especially characteristic of the Pelecypods, and being formed by the same or similar glands to those secreting the shell resemble it in character; the concretions of *Arca* are usually violet, of *Pinna* rose coloured, and in other groups they likewise appertain in colour and structure to the interior of the particular shell to which they belong, the species with porcellanous shells producing concretions resembling marble, while those from nacreous shells display a more or less brilliant opalescent lustre and are distinguished as Pearls.

Pearls are perhaps the most valuable production of the mollusca, and, before the systematic and successful prosecution of the Oriental pearl-fisheries, were very largely derived from the *Unio margaritifer*, a species which exists not only in the British Isles, but throughout the northern circumpolar regions, the production of pearls being formerly so especially identified with the Unionidæ, that the name *Unio*, signifying a pearl, was applied to the typical genus.

Pearls, as well as the kindred but less beautiful porcellanous or fibrous concretions, consist of successive and alternating layers of calcareous and chitinous matters, deposited around any irritating extraneous particle or particles which may have gained entry amongst the delicate glandular tissues. In some localities the eggs or bodies of *Atax*, *Bucephalus*, or other of the minute internal parasites may be the predisposing cause, in others a grain of sand or other foreign irritant substance may furnish the nucleus and necessary stimulus for secretory activity, the intrusive atom becoming enclosed by successive accretions until it may eventually attain such a size as to preclude the closure of the valves and cause the death of the animal.

But from whatever causes they may originate, these deposits of pearly matter are produced at the expense of the shell, and it is, therefore, not surprising to find that the shells of pearl-bearing individuals are often deformed, and can usually be recognized by the asymmetry of their valves, the constriction of the lower margin of the shell, or the presence of radiating grooves or ridges, as it is seldom that a regularly formed shell contains a pearl.

Pearls may be formed in almost any part of the tissues, in the substance of the mantle, between the body and the gills, between the gills and the mantle, or between the mantle and the shell; sometimes they are found singly, at others several occur together, either free or adherent to the interior of the shell or to each other.

The shape too is very variable and may be spherical, ovoid, pyriform or irregular, perhaps dependent upon the character and shape of the nucleus around which the pearl is formed, although perfectly spherical pearls are affirmed to always originate by the enclosure of the irritating particle within an ampulla or cyst filled with an organic fluid, which undergoes lamellar condensation around the intrusive atom, the interstices of the chitinous layer becoming filled with a calcareous deposit. The delicate wall of the cyst afterwards becomes ruptured and the incipient pearl or concretion is freed, so that the periodic deposition of pearly substance can continue to be uniformly and evenly applied.

If a pearl lying loose in the tissues becomes lodged between the mantle and the shell it may become attached to the inner surface of the shell by the successive accretions of pearly matter, and thereby lose its spherical form and the lustrous iridescence characterizing free pearls.

The most valuable and esteemed pearls are of a lustrous white, delicately tinged with azure or salmon, or those of an exquisite rose color. The iridescence, which gives to pearls their greatest charm, is due to the diffraction of the light by the partially transparent and minutely corrugated layers forming the exterior of the gem; the thinner and more transparent these layers the more beautiful the lustre, the superiority of the Oriental pearls in this respect being the reason of their greater beauty and value compared with British pearls. Besides the corrugated furrowing, there are a number of fine dark lines $\frac{1}{7700}$ of an inch apart, which run in different directions or from pole to pole, and may add to the lustrous effect.

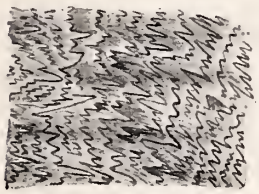


FIG. 617. — Surface of Pearl, highly magnified, showing the minute undulations upon which the pearly lustre depends (after Tryon).

Unlike precious stones, pearls, being animal products, quickly fade and decay and only great care keeps them in good condition for any length of time; they will tarnish when worn next the skin or even when enclosed in a jewel box. When dim and lustreless, their brilliancy can, however, be restored by "peeling," a process skilfully practised by the Chinese, who use for this purpose a keen knife, files, pearl powder and a scrap of leather, the final polishing being given by the leaf of a particular plant.

Pathological causes may also beget an irritation which is liable to induce, in the substance of the adductor muscles, the formation of small and irregularly-shaped concretions, which are called Sand or Seed pearls and used for enriching embroidery, etc.

British pearls have been celebrated from the earliest times for their size and brilliancy, the crowns of the ancient British kings being encircled with pearls, as shown by their coinages, and Suetonius records that the fame of their loveliness was the chief inducement that led Julius Cæsar to undertake the conquest of this country to obtain them. Pliny and Tacitus concur in stating that he dedicated and hung in the Temple of Venus Genetrix, a buckler made of British pearls, and though Pliny remarks that the pearls used were small and poor, yet, on the other hand, the Venerable Bede comments especially upon the orient lustre and brightness of the native pearls, while in modern times Dr. Leach has stated that pearls from our *Unio margaritifer* were often sent to India and re-imported to this country as Oriental pearls.

In North America the prehistoric Indians carried on the *Unio* pearl fishery upon an extensive scale, especially in the Scioto and Miami valleys. The robes of their great chiefs were enriched by a lavish display of exquisite pearls, which were always pierced by means of red-hot copper wire to ensure secure attachment. These treasures were always buried with their owners, and hundreds of thousands of what had been large and magnificent pearls have been obtained from the burial mounds of Ohio, Georgia and other places; these are, however, now worthless, except as curiosities, being blackened and spoilt by fire, perhaps from being thrown into the flames of the altars, or have become rotted and cemented into masses by water filtering to them through the soil during their long burial.

The Chinese who, in the thirteenth century, discovered the mode of producing pearls, also obtain pearl-covered images or other objects by introducing into the shell of the living mollusk small models of the figure or shape required, which become in due time covered by a pearly layer or deposit.

European attempts to produce pearls have not been financially successful, although the celebrated Linné owed his elevation to the nobility partly through his efforts to produce pearls artificially, by, it is supposed, piercing small holes through the shell and introducing thereby grains of sand to form the nuclei of the desired pearls.

The *Unio* pearl-fisheries are still somewhat desultorily carried on in various parts of the British Isles, North America, Germany and a few other countries, but were formerly of much greater importance and extent.

Even at the present day the fisheries still existent in various Irish and Scotch rivers occasionally yield valuable pearls, but during the eighteenth century the Tay fishery was very productive, the value of the pearls found therein from 1761—1764 being about £10,000.

The Welsh pearls were also noted for their lustrous beauty, the Conway being said to have furnished a pearl of especial purity which Sir Richard Wynne presented to Queen Catharine, and which, according to Reeve, is now set in the crown of Queen Victoria, although the Keeper of the Regalia states there is no mention of such a gem in the description of the Crown jewels.

The Pigment Cells (*pigmentum*, paint or colour) are distributed throughout the body, but are perhaps most plentiful in the connective tissue subjacent to the external epithelium, and in the testaceous species are chiefly congregated at the mantle-margin, passing insensibly into calcic and mucous cells, the three mutually intergrading as is shown in *Arion rufus*, *Limax flavus* and other species, in which pigment is associated with and stains the dermal mucus and assists to give the body its distinctive tint; similar effects are exhibited in *Agriolimax agrestis*, in which the functional relationship of the mucous and lime cells is exemplified by the limey mucus they so plentifully exude.

This expulsion of colouring and other matters from the body may be regarded as a true excretory function, quite analogous to that seen in the periodic moulting of the feathers in birds and the shedding of hair in animals, as Uric acid and other colouring matters are waste products of the organism, which have probably been seized upon by the phagocytic cells and carried to the external surface of the body; the exhaustion of the supply of colouring matters at the surface by its long continued or too copious exudation with the slime, when the animal has been closely confined for a length of time or greatly irritated, probably accounts for the instability of colouring in adult slugs. Under such circumstances *Limax flavus* is said to pass rapidly from light yellow to dull olive-green, and *Arion ater* has been recently observed by Mr. Gain to pass in a very short space of time from orange-yellow, through chocolate-brown to grey, tinged and spotted

with orange, with grey lateral bandings, before again eventually reverting to the orange-yellow colour which distinguished it when first found.

Pigment may be a natural product of the organism, or an inherent characteristic of the substances composing the body, as exemplified by the deep dull red colour of hæmatin, the base of hæmoglobin, and therefore not dependent on the action of light, which is not really essential to its production, as is demonstrated by the varied colouration of the internal organs and by the brilliant tints of many deep sea animals which permanently dwell in cimmerian darkness. Its distribution and arrangement is, however, largely influenced by selective and other forces, and also dependent on the character of the tissues and the nature of the general environment, being modified by age, the amount of heat or cold, moisture or drought, food, light or darkness or, in fact, by anything which affects the physical constitution of the body and may by retarding or accelerating chemical changes or combinations produce changes of colour.

Age has great influence on colouring, *Limax flavus* and other species becoming darker with advancing age, and this chromological change assists us to a better understanding of a probably more primitive colouring, as the accepted law of coloration in animals is for the young of allied species or genera to bear more resemblance to each other and to their common ancestor than the adults do, the successive changes undergone during growth probably hinting at the series of adaptations necessitated by environment during their specific life.

In *Arion minimus*, one of the most primitive species of that genus, a greenish tint is indicated by its early development, as probably an ancient colouring of that species, this colour changing from time to time during growth, through yellow with slate coloured dorsal and lateral lines, to nearly uniform yellowish-white before finally becoming grey on the back, with greyish-yellow sides and yellower caudal region, the mantle assuming a somewhat uniform dull greyish-orange colour.

Arion ater has also been noted to undergo even more remarkable and varied colour changes during growth, both probably indicating adaptations to stations successively occupied during the extension of their range, the observed scale of changes undergone in dermal coloration by the Arions and other groups thus suggesting the probable route of their evolution to the attainment of their present tints, and although the genetic sequence of colours in the mollusca has not yet

been satisfactorily worked out, it has probably diverged and varied in response to environment from a comparatively simple and more or less uniform tint of animal and shell towards the more striking and distinct colours they now so frequently exhibit, the more fugitive and advanced colours being the result of greater chemical activity and change amongst the constituents of the body, and are probably those most recently acquired and which have not yet become an integral and permanent part of the organization.

Food has been undeniably demonstrated to modify the colours of certain insects and birds, and it is probable that a particular diet will to some extent modify and influence the intensity and character of the pigmentation in the mollusca. Mr. Hawkins, in "The Naturalist" for February, 1899, has published some practical observations on the apparent influence of food upon the colours of the shells of Helices, which it would be of the greatest interest to confirm or refute.

Cold has been demonstrated to inhibit the formation of the red pigment, but to be favourable to the development of the black, which is generally due to Melanin, a substance which is practically identical with the colouring matter of the cephalopod ink and is usually found in minute particles in the dermal epithelial cells as well as in those of the other parts of the body, its greater abundance being correlated with superior physical vigour, as it is in relation to and in a great measure dependent upon the mass of blood in the organs from which it is secreted and deposited in the external integument in response to external influence, the effect of cold being demonstrated by Simroth to induce darkness of colouration in the slugs, especially if they are subjected to its influence during spring, at the period of their most active growth and development.

A further confirmation of this law of colouring is afforded by the observation of the Rev. Dr. Norman of the darkening of *Agriolimax agrestis* under the diminishing temperature of autumn and by the known fact that *Limax cinereo-niger*, the northern race of *Limax maximus*, is often totally black, while in warm Italian regions the species develops a series of brilliantly coloured and strikingly marked forms.

Limax marginatus (Müll.) offers still more striking confirmatory evidence of the effect of cold and moisture in inducing melanism. In the north and north-western parts of this country and on mountain sides this species becomes darker in colour and loses the glaucous and translucent aspect which is its usual characteristic on

warmer and drier ground. On the Italian mountains the transition from the ordinary translucent glaucous specimens found in the valleys to the intensely dark opaque specimens inhabiting the cold and cloudy mountain regions can be clearly traced, and although these sombre forms may not be limited geographically to particularly humid regions or cold northern latitudes, yet their appearance is always indicative of the local or transient peculiarities of their environment.

Heat principally affects and increases the formation of the red pigment and under artificial conditions has been experimentally demonstrated by Simroth to inhibit the dermal disposition of the black pigment in *Arion ater* and *Limax maximus* and also to favour the development of albinoes, the individuals, however, only remaining albine under a continuance of the warmth, while other specimens from the same batches of eggs reared under more natural conditions acquired the colourings characteristic of the species.

The red colouring matter, which has been shown to be to some extent dependent upon warmth for its production, has been shown by Simroth to be probably a warning colour in *Arion*, as many creatures to whom he offered *Arion rufus* as food either totally rejected it or ate only the viscera, and as the red pigment is probably a waste product of the tissues, discharged by the dermal glands, this effect is not improbable.

The pigmentation of the animals of our land and fluviatile mollusca does not generally exhibit any remarkable differences in the distribution of the colouring, the variations being chiefly confined to differences in the intensity of the general colouring; the greatest variety is shown by the naked species, which being fully exposed to the full effects of external influences, are more quickly affected by and responsive to changes in their environment and therefore exhibit greater diversity in the external pigmentation of the body.

The Protective Resemblance of the animal or shell of various species to some natural object of the environment is due in a great measure to external coloration, the specially imitative mode of its distribution or arrangement being probably gradually acquired by the preservation and perpetuation of those individuals most closely simulating the particular object. A strikingly coloured animal or shell, strongly contrasting with the surroundings amongst which the creature exists, must, unless it is otherwise protected, inevitably be more easily detected by its enemies, thus tending to the elimination

and destruction of the more conspicuous specimens, and the preservation of those variations which harmonize most closely with the environment, while heredity will assist in the perpetuation of those individuals, which either by colouring, form, or habit are most difficult to distinguish amidst the surroundings amongst which they habitually live.

Amongst exotic species many striking instances exist of the protection afforded by resemblances to other objects, and although in our own more prosaic country we can scarcely hope to have examples of so striking and beautiful a character, they are yet of the highest interest and probably of vital importance to the welfare of the different species.

Amongst the slugs, Mr. G. Sherriff Tye has recorded the similitude of *Arion hortensis* and *Agriolimax agrestis* to the fallen bloom sheaths of the Black Poplar (*Populus nigra* L.). This resemblance is affirmed to be sometimes so perfect that the keel, pallial line, and even the corrugated surface are so strikingly simulated as to render the deception quite complete, and Dr. Scharff and others have recorded the striking similarity between the animal of *Geomalacus maculosus* and the foliage of *Frullania dilatata* and other liverworts and lichens, amongst which it lives and finds its food, while other species have been shown to closely resemble other familiar and inedible objects.

Amongst land shells, *Buliminus obscurus* has long been noted for an analogous habit to that of the burrowing bivalves, and its adventitious protective covering does undoubtedly vary according to the situation inhabited. In woods where the trees are clad with lichens, this little shell is similarly clad and then resembles little moss-covered knots or excrescences upon the bark of the trees; or, if found on dry hedgebanks or on roadside trees or walls it often bears a most natural resemblance to a misshapen piece of mud or stone.

Protection is probably also secured by *Helix fusca* through its wonderful resemblance to the decaying capsule or seed-case of the Red Campion *(Lychnis diurna)*. This resemblance is, according to Mr. Masefield, so faithful as often to require a close scrutiny to determine whether the doubtful object be a snail or a seed pod, as this species is the exact colour of the capsule when wet—a transparent horn colour, and the bottom of the seed-case being light-yellow exactly reproduces the appearance of part of the viscera of the mollusk as seen through the shell.

Mr. L. E. Adams has recently observed that, on the sandhills at Sandwich, *Helix cartusiana* is chiefly found upon the Hound's Tongue *(Cynoglossum officinale)*, clinging to the withered stems and so closely simulating the clusters of burr-like seeds that it is difficult to distinguish the shells in the sunlight.

Limnæa when crawling on the bed of a stream or pond assimilate in a remarkable way to their surroundings, and the darkly mottled mantle which often shows dimly through the shell does not render them more perceptible, but rather tends to their closer approximation with the appearance of their surroundings.

The *Viviparidæ* are often found so thickly coated with mud that no portion of the actual shell can be seen, and the resemblance to, and assimilation with, the bed of the canal or river is complete. This incrustation often contains fragments of plant tissues and may also be rich in *Algæ*, chiefly represented by numerous species of Diatoms. *Oscillatoriæ* are sometimes equally plentiful in the deposit and frequently, in the living condition, imparting a greenish tint thereto.

Amongst bivalves the tufaceous or muddy deposit upon the protruding posterior part of the valves is well known to all conchologists, who readily acknowledge the perfection of the disguise, which is only penetrated by the opening of the valves and the protrusion of the siphons. Often this incrustation becomes the seat of growth for *Algæ* or other water plants, and the difficulty of detection is correspondingly increased.

The Nephridia (νεφρός, kidney), Renal organs or Kidneys, known in Gastropods also as the Precordial gland, are typically paired and dorsally placed excretory organs, always symmetrical in symmetrically organized animals with paired gills, and metameric in *Nautilus*, in which the respiratory organs have a serial character, but single in most Gastropods in correlation with the loss of the moities of many other of their primitively paired organs.

These organs in the mollusca assume a variety of forms in exotic genera or the constituent parts may permeate amongst the various organs of the body; usually, however, they consist of a pair of tubules, each of which is closely folded upon itself, forming a loop, connected proximally by the ciliated reno-pericardial funnel with the base of the pericardial cavity or secondary cœlom, with which they are always in intimate relation. The proximal tract or limb is enlarged and sacculate with rich vascularization and constituted by brownish or

yellowish tissue, containing numerous cœca and projecting glandular lamellæ or trabeculæ, overspread by a densely ciliate layer of secretory cells, which fill up the lumen of the organ and contain a yellowish or greenish fluid with concentrically formed concretions, similar to those in the renal organs of other animals, the rupture of the cell-walls allowing their escape.

Fig. 618.—Kidney cells of *Helix arbustorum* L., highly magnified, showing the contained Uric acid concretions (after Boll).

The deoxidized and impure blood returning from its circuit of the body, laden with the waste products of the oxidation of the tissues, joins with some arterial blood from the lung and circulates within the kidneys before reaching the respiratory organs, thus constituting a portal circulation which partially purifies the blood by eliminating therefrom the nitrogenous waste matters, in the form of Urea, Uric Acid, Calcium-phosphate and other substances, amongst which Ammonia, Creatinin, Tyrosin, Leucosin, Guanin, etc., have been recorded.

The excretory substances vary somewhat in character in the different groups, the Pelecypoda chiefly expelling Urea, which is formed by the more or less complete oxidation of the anatomical elements of muscular tissue and is produced most plentifully during periods of abstinence or food scarcity; while many Streptoneures excrete Uric acid, which results from an incomplete oxidation, due to the blood being surcharged with peptones which the tissues are unable to assimilate, a state consequent upon a plethora of food.

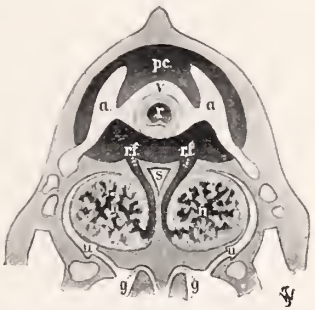


Fig. 619.—Diagram formed from several combined transverse sections through *Anodonta*, showing the relative positions of the kidneys or renal organs and their ducts (after Griesbach).

n. nephridia, with *r.f.* reno-pericardial funnels and *u*. ureters; *pc*. pericardium; *a*. auricle; *v*. ventricle; *s*. vena-cava or blood-sinus; *r*. rectum; *g*. genital ducts.

In the Pelecypoda the kidneys are known as the Organ of Bojanus, the simplest form being found in *Nucula* and other Protobranchiates, in which they consist simply of a pair of folded and separate cylindrical sacs, placed beneath the pericardium and in front of the posterior adductor, each sac possessing a spacious lumen and similar secretory walls throughout its extent, the pericardial

and excretory orifices of each gland being placed anteriorly, the excretory opening being confluent with or near the genital aperture and the excreta, especially in the more archaic genera, being expelled in a fluid form.

In the more advanced genera, as in the *Unionidæ*, etc., the secretory walls become more complicated and the glandular surface augmented in the proximal or ventral limb, to which it becomes chiefly restricted,

FIG. 620.

FIG. 621.

FIGS. 620 and 621.—Transverse sections through two regions of the renal organs of *Anodonta cygnea* (L.), highly magnified (after Rankin).

k. secretory section of kidneys; *u*. ureter; *b.s*. blood sinus; *f*. foot; *c.pl.v.c*. section of cerebro-pleuro-visceral commissure.

the distal or superior limb forming the duct to convey the secretions to the exterior and opening into the mantle cavity, always above the cerebro-pleuro-visceral commissure; but sometimes, as in *Sphærium*, etc., within a common urogenital cloaca; in most groups, however, the renal and genital apertures are distinct, although the kidneys themselves, as well as their ureters, communicate freely with each other, especially in the more specialized forms.

In the Streptoneura the primitively paired character of the kidneys still persists in a more or less distinct form in the Diotocardia, yet the right kidney, though still connected with the pericardium and mantle-chamber, has entirely lost its renal function and has become utilized as a channel for the conveyance to the exterior of the genital products; the left kidney, however, still retaining its exclusively renal and secretory character.

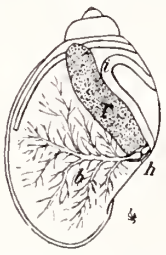


FIG. 622.—*Succinea putris* (L.), × 3, showing position of kidney or renal organ.

r. renal organ or kidney; *b*. pulmonary plexus; *i*. intestine; *h*. heart.

In other Streptoneures the left kidney is alone present in adults in correlation with the retention of the moieties of other paired organs, and is situate to the left of the rectum, though actually traversed by that organ in some genera. The right kidney has, however, also been detected to be transitorily present in *Vivipara*, etc., during embryonal development, its ureter, however, persisting in the adult, but acting solely as a genital duct.

In the Euthyneures there is also but a single kidney, the representative of the right kidney of the hypothetical primitive mollusca and of the Pelecypod; it is placed upon the roof and in the rear of the pulmonary chamber, between the pericardium and the rectum and is of the parenchymatous type, the complex folds and lamellæ of the walls projecting into the cavity and often quite filling up the lumen of the organ.

Fig. 623. — Longitudinal section through the kidney of *Agriolimax agrestis* L., × 50, showing its complicated structure (after Hanitsch).

The Ureter is the ciliated thin-walled excretory duct of the kidneys; it is paired in the Pelecypoda in correspondence with the paired glandular sections whose products they discharge, their apertures being usually placed above the base of the foot and opening into the supra-branchial or cloacal chambers, in close vicinity to or in conjunction with the reproductory orifice.

The duct of each kidney is folded back upon the secretory section and are separated by the Vena-cava, but they usually communicate by means of the oval inter-renal space near their outlets; they represent the Primary Ureter of the Gastropoda.

In those species which retain their primitive organization the genital glands having no special ducts discharge their products into the nephridia, which are transmitted to the exterior by the ureter.

In our Streptoneura the kidney is placed at the rear of the mantle cavity, the slit-like excretory aperture, which characterizes many of the groups, opening directly into the pallial cavity, although in *Vivipara* and *Valvata* the orifice becomes a tubular and elongated duct, which is distinguished as the Primary Ureter, a name applied to the first direct excretory tract originating at the kidney, and discharging the waste matters towards the exterior.

In the Euthyneures the urinary duct has a more complex development and the various stages are to be observed leading from a simple aperture, opening directly into the pallial chamber, to a long and almost sinuous duct, conveying the renal secretions quite to the exterior of the body.

The Primary Ureter or renal efferent duct is represented by a simple orifice in certain species of *Planorbis*, but is well developed and prolonged towards the pulmonary orifice in most other Basommatophora, in *Cionella*, *Pupa*, *Buliminus* and some of the more primitive Helices, or, instead of extending directly towards the

aperture, it may assume a backward direction, fusing with the wall of the secretory sac and opening at the extreme rear of the mantle-chamber, as in *Testacella*, etc., while an intermediate stage leading to the highest development of the ureter is seen in the formation in some Helices of a more or less open channel, leading from the aperture of the backwardly directed primary ureter in the rear of the mantle-chamber to the pulmonary orifice; this channel eventually becomes

FIG. 624. FIG. 625. FIG. 626. FIG. 627. FIG. 628.

Diagrams illustrating the development of the Ureter in the Gastropoda (after Lang).

r. kidney or renal organ; *p.u.* primary ureter; *s.u.* secondary ureter; *r.* rectum; *p.o.* respiratory orifice; *h.* heart, within its pericardium.

FIG. 624.—Portion of respiratory chamber with the excretory renal orifice existing as a simple papillar opening, as in certain Planorbes, etc.

FIG. 625.—Shows the elongation of the simple excretory orifice into a long and definite duct, the Primary Ureter as in the Basommatophora and certain Streptoneures, etc.

FIG. 626.—The Primary Ureter is directed backwards and adherent to the kidney, opening at the back of the respiratory cavity, as in *Testacella*, etc.

FIG. 627.—Shows the formation of an open channel leading to the exterior from the renal opening in the rear of the chamber, as in certain Helices.

FIG. 628.—Shows the formation of the open channel into a definite duct, the Secondary Ureter and its junction with the rectum, as in our most highly organized Helices, etc.

closed and forms a definite duct, distinguished as the SECONDARY URETER, the name applied to the differently directed tract in continuation of the backwardly directed primary ureter of the *Testacellæ*, but following a different direction, parallel with and opening into or near the rectum, as in *Arion*, *Amalia*, *Limax*, *Vitrina*, *Hyalinia* and the more highly developed Helices.

The PRONEPHROS (πρό, before; νεφρος, kidney), Wolffian bodies or provisional renal organs, known also as Stiebel's canals, are possessed by many embryonic mollusca and are especially characteristic of the Trochosphere stage of larval life, as they atrophy and disappear before the close of the Veliger phase of development.

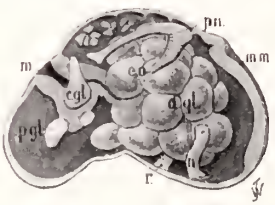


FIG. 629.—Embryo of *Planorbis corneus* (L.), seen from the left side, × 100 (after Fol.), showing the Pronephros or primitive kidney.

pn. pronephros or primitive kidney; *c.o.* its external orifice; *m.* mouth; *r.* rectum; *n.* nephridium or permanent kidney, also showing external orifice; *d.gl.* digestive gland; *m.m.* mantle margin; *c.gl.* cerebral ganglion; *p.gl.* pedal gland.

They arise by ectodermic invaginations in the anterior region of the body, behind the velum, but considerably in advance of the later and permanent kidneys of adult

life, they are always paired and are best developed in the aquatic pulmonates, consisting of anteriorly directed V-shaped tubes, opening into the body cavity; the cephalic or longer limbs are richly ciliated and directed towards the Velar area, the shorter or pedal limbs being unciliated and directed towards the foot; the cellular dorsally-placed apical sacs contain concretions and open exteriorly at the sides of the neck.

In the Streptoneures these organs are formed by a mass of excretory cells, with numerous vacuoles containing concretions placed at each side of the body. At a later stage the vacuoles unite to form a cavity filled with a brown granular mass.

The larval kidneys have been observed in many Pelecypoda, each being constituted by a deeply situate ciliated canal and a more superficial part, with an external opening at the postero-ventral side of the cephalic region, and an internal one within the body cavity.

The Pericardial Gland (*περὶ*, around ; *καρδία*, heart) or Keber's organ has an apparently important excretory function in many mollusks, and is a thick and spongy glandular differentiation of the pericardial epithelium covering the walls of the auricles and closely connected with the vascular system, but always constituted by flattened cells, destitute of the concretions characterizing the renal cells.

In the Pelecypoda it arises as a pericardial investment of the auricle or at the anterior angle of the pericardium, which would appear to be its most primitive position, and though often found as a proliferation of the anterior pericardial walls, is not always developed at the same place or in exactly the same way. It is an organ quite analogous to the kidneys, having a rich sanguine irrigation, mainly by the arterial blood returning to the auricle, extracting therefrom a more acrid secretion than that eliminated by the kidneys, which, in *Cardium* and other marine genera, has been determined to be Hippuric acid; this is discharged into the pericardium and flows through the reno-pericardial funnels into the kidneys and thence to the exterior by the ureters.

Except in *Nucula* and other archaic genera, the pericardial glands are almost universally present in the Pelecypoda in the form of paired reddish glands, upon the auricular walls within the pericardial cavity, or as an agglomeration of glandular tubules protruding from the anterior corner of the pericardium into the mantle lobes, both these forms being found among the species of our fluviatile genera.

Among the Streptoneures the gland in the Diotocardia maintains its primitive position upon or near to the walls of the auricles, the pericardial cavity being contracted by its proliferations, but in the Monotocardia it is found upon the internal pericardial walls.

The CONCRETIONARY GLAND is characteristic of *Cyclostoma*, although organs of somewhat similar aspect and probably analogous functions exist in *Bithynia tentaculata* and doubtless other species. The gland is to be regarded as a secretory organ and store-house for Uric acid and probably other waste substances, and was surmised by Garnault to have been acquired by the ancestors of the *Cyclostomidæ* when they relinquished aquatic for terrestrial life, the more frequent periods of rest necessitated by the greater fluctuations of temperature, hindering the action of the kidneys, and the Uric acid accumulating within the concretionary gland, to be afterwards re-absorbed and passed away from the system by the ureter when active life was resumed, as the concretionary gland has no excretory duct nor does it communicate either with the pallial cavity or the digestive tube.

FIG. 630.—Follicle of Gland of Concretion of *Cyclostoma elegans* (Müll.), highly magnified (after Garnault).

The gland is a greyish or brilliant white organ, occupying a dorsal position beneath the kidney and composed of dense tufts of simple or branched follicles, some of which may be two millimetres in length, disposed among the intestinal convolutions, all being bound together by loose connective tissue and encompassed by a rich vascular plexus.

This organ is variously developed, individually and seasonally, being more pronounced in autumn than in spring, the follicles at the former time being filled by multitudes of solid sphæroidal concretions formed by concentric lamellæ, disposed around one or more nuclei. The colour of the gland is entirely dependent upon the number of concretions present in the follicles, the organ showing the characteristic brilliant white colour when they are numerous and being greyish when the contained concretions are less plentiful.

FIG. 631. — Concretion from Concretionary Gland of *Cyclostoma elegans* (Müll.), highly magnified (after Garnault), showing the concentric lamellar structure.

The concretions are translucent in *Cyclostoma costulatum*, but only occasionally so in *Cyclostoma elegans*, they may, however, be rendered transparent and their complex structure demonstrated by immersion in weak alkaline solutions, Ammonia, Potass or Soda water. They dissolve instantly without effervescence in Sulphuric acid, and the various reactions show the concretions to be almost entirely composed of Uric acid.

The interspaces between the concretions are filled with a grey mass of immobile Bacilli, three to four μ long, which however exhibit Brownian movements. They are variable in size and shape and often united together in pairs, and their constant presence in this closed cavity containing so much alternately deposited and re-absorbed Uric acid, would seem to indicate symbiotic action, the bacilli having probably some important function either in connection with the deposition or the re-absorption of the Uric acid concretions.

FIG. 632. — Bacilli of Gland of Concretion of *Cyclostoma elegans* (Müll.), highly magnified (after Garnault).

The LYMPHATIC GLAND (*lympha*, water) or Spleen, the formative organ of the amœbocytes or white blood corpuscles, though present in our land and fluviatile species, is not so distinctly localized as in the Opisthobranchs, the lymphatic cells being more generally diffused throughout the connective tissue, though usually most numerous and active in or near the respiratory organs, especially along the course of the afferent cardiac vessels and upon or near the auricle, and hence it has been termed the "Gland of Auricle" by some observers.

Although the grouping of the lymphatic cells is so variable in character, their aggregations are always constituted by a layer or stratum of connective tissue, crowded with nuclei, which become invested by protoplasm containing refractive ferment granules, the amœbocytes eventually passing through the meshes or interstices of the connective tissue and falling into the blood stream.

In *Dreissensia* this sanguineous or blood-making gland, as it has been termed, is in the gill itself, close to the afferent vessels, but in the Gastropoda it varies greatly in position. In *Limax* and *Helix* the gland occurs as a thick stroma surrounding all the efferent pulmonary vessels; but in the *Limnæidæ* the gland is not distinctly separable from the pulmonary vessels. In our Streptoneures the lymphatic organ may have a dual development, being not only represented along the

basal portion of the gill and opening into the branchial vein, but a specialized area of connective cytogenous tissue, the Nephridial gland, invests the renal vascular plexus, and encloses lacunar spaces, which communicate with the auricle, the amœbocytes passing into the blood within its cavity.

The amœbocytes and the large vesicular wandering cells, known as the "cells of Leydig," take up and absorb sickly and degenerating tissue and foreign bodies which have gained entrance into the system, indigestible or insoluble particles becoming encapsuled and removed from the circulation, a process of excretion which occurs in many animals; many of the mucus, pigment and other cells so numerously present in the external tissues are wandering cells, probably conveying their contents towards the surface of the body, they also act as storehouses for the accumulation of a reserve store of nutriment in the form of glycogen.

Many of our species, owing to the energetic phagocytary action of their amœbocytes, can withstand, without apparent injury, the introduction into the body of many poisonous substances or large quantities of bacterial disease germs. Our *Helix pomatia* has been demonstrated to successfully resist the deleterious presence of such organisms or substances within the body, the bacteria soon becoming collected together in the most delicate parts of the lung, which are essentially phagocytic in function.

The Muscular System embraces the organs by which the movements of the body are accomplished, under the stimulus of the efferent nerves from the various ganglionic centres.

This power of motion or movement is possessed by every animate creature, but in the lowliest organisms where there is little differentiation of parts, the whole body is mobile and contractile, constantly changing in shape by the incessant retraction or protrusion of different parts of the body substance in the form of Pseudopodia (ψευδής, false; ποδ- foot) a primary form of movement exhibited by the amœbocytes or white blood corpuscles, present in the blood of the mollusca and other animals.

Cilia (*cilium*, an eye-lash) and Flagella (*flagellum*, a whip-lash) are finer and more delicate prolongations or extensions of the body substance, but more permanent in character; they form more advanced organs of locomotion, particularly characteristic of the Infusoria and of the Veliger and Trochosphere stages of the molluscan embryo.

As we ascend the scale in the animal kingdom or arrive at a later stage in the development of the mollusca, true locomotor and other muscles become more distinctly differentiated and it becomes due to their alternate contraction and extension that movements are effected.

Muscles in most animals are what are popularly known as flesh, and are constituted by bundles of fibres collectively enclosed by a strong membrane, each constituent fibre being surrounded by a thin sheath of connective tissue and arranged with its length parallel with the direction or pull of the muscle, and also connected with a nerve cell, whose stimulation causes the contraction of the filament and draws together the parts to which the opposite ends of the muscle are affixed.

Muscles may be Voluntary or Involuntary, according as they are or are not under the control of the animal, although it is probable that many apparently voluntary muscular movements are merely reflex actions in response to external stimuli.

Involuntary or Unstriated Muscles are predominant in the molluscan organism, but are more especially characteristic of the splanchnic muscular layer, and are composed of greatly elongated, smooth and unstriped muscle-fibres, which generally contract slowly and rhythmically, as exemplified in the regular and periodic movements of many of the internal organs.

Fig. 633.—Unstriated muscle fibre from foot of *Neritina fluviatilis* (L.), highly magnified (after Boll).

The Voluntary or Pseudo-striate Muscles in the mollusca are chiefly retractors, but also embrace the integumental muscles, the protractors, the levators and the extensors, but the protractor and other muscles are in their action usually subsidiary to concentrated blood pressure in causing the protrusion of the extensible organs of the body.

Fig. 634.—Pseudo-striate muscle fibre from buccal bulb of *Neritina fluviatilis* (L.), highly magnified (after Boll).

In the mollusca, the Voluntary muscles show transverse granulation or are entwined by spiral fibrillæ which give to the muscular filaments a striated aspect. This incipient transverse striation is especially characteristic of molluscan voluntary muscle, being present in the buccal mass of many Gastropods, and in the adductors of the Pelecypoda. It is the biological expression and mechanical result of their increased function and of the numerous waves of contraction of the muscle substance, as the striation is incomplete

or wanting in sluggish mollusks, and most pronounced in the more active forms.

The general character of the musculature of the mollusca is, in a great measure, dependent upon the development of a protecting shell, which furnishes a firm attachment to the great retractor muscles of the body, by whose action the animal is withdrawn within its shelter, the columellar muscle of the Gastropods apparently representing the more numerous retractors of the Pelecypoda.

The Columellar Muscle in the testaceous Gastropods is the principal retractor of the body, its presence being typically correlated with the possession of an external shell into which the body may be wholly or partially withdrawn for protection; it also constitutes the sole connection between the animal and its shell, the muscle being organically fixed to the shell-axis or columella and running forward beneath the respiratory cavity, the constituent glistening white fibres dividing and becoming distally distributed among and interlacing with the musculature of the foot, chiefly in the longitudinal median region; it also gives off from its upper surface subsidiary yet powerful anteriorly-directed muscular strands which are known as the cephalic retractors.

The Cephalic Retractors (κεφαλή, the head) form a very important part of the musculature of the body, the constituent parts being distinguished as Pharyngeal or Tentacular retractors, according to the function they discharge.

Fig. 635.—Cephalic retractors of *Amalia gagates* (Drap.)×2, showing the arrangement of the pharyngeal and tentacular retractor muscles.
p. pharyngeal retractors; *t*. tentacular retractors.

The Pharyngeal or Buccal retractors are always median and may be formed of paired and slightly divergent muscular slips or of a more powerful single muscle, but they always pass through the nerve ring to become fixed to the buccal bulb by divided or by simply expanded extremities.

The Tentacular retractors are always paired, corresponding muscles being present for the right and the left sides of the body, which may be united posteriorly with the great columellar muscle or, as in certain of the nude species, may arise independently from the integument. They also exhibit special minor

features which are more or less specifically or generically characteristic, the retractor of the right ommatophore, in many species, passing between and separating the penis and the vagina, while the retractor of the right lower tentacle passes beneath the penis, which is thus confined within the loop the retractors form.

Althongh the cephalic retractors are less specialized in the Streptonenra than in the Stylommatophora, yet the columellar retractor in the former group exhibits a special modification, due to the presence of the operculum upon the dorsal surface of the foot, the latter, however, in correlation with the acqnirement of paired invaginable tentacnla, exhibit greater complexity anteriorly, the tentacular muscles functioning for the independent or collective withdrawal of these organs within the body; more delicate mnscular strands may also be given off to other organs to facilitate their retraction.

The cephalic muscles vary in complexity and may for the purposes of study be divided into three groups: Dichorhiza, Monorhiza, and Trichorhiza, based upon the number of their points of attachment to the colnmellar muscle or to the integument in the nude species.

The Dichorhiza (δίχα, in two parts; ῥίζα, a root) or two-muscled species exhibit the simplest form of cephalic mnscnlatnre possessed by our Gastropoda, and wonld appear to be especially characteristic of the Streptonenra and the Basommatophora, being quite deficient of any trace of tentacular retractors in correlation with their possession of non-retractile tentacles; the pharyngeal retractors, which alone are present, are two distinctly separated muscular strands, arising from the great columellar mnscle and affixed to the buccal bulb. In the Basommatophora the penial retractors may also emanate from the columellar muscle near the same spot.

Fig. 636.—Cephalic retractors of *Limnæa peregra* (Müll.), × 3, illustrating the section Dichorhiza, and incidentally showing the origin and character of the penial retractors.

c.m. columellar muscle; *p.r.* pharyngeal retractors; *r.* penial retractor; *p.s.* penis sheath; *v.d.* vas deferens.

The Monorhiza (μόνος, single; ῥίζα, a root) are those forms in which the muscles for the retraction of the head, tentacles and adjacent organs are combined together medially to form a common stem at their point of origin from the columellar muscle. This group embraces the Helices, certain *Hyalinia*, and the genera *Amalia*,

Agriolimax, *Limax*, *Succinea*, etc., and in respect to this portion of their organization these genera are less highly specialized than *Arion*, *Testacella*, etc, which appertain to the group Trichorhiza.

The tentacular retractors are uppermost and originate most posteriorly upon the columellar muscle, and in some species midway in their course give off muscular strands to the anterior region of the foot. Before reaching the base of the tentacles each muscle divides, the larger branch entering the upper tentacles or ommatophores, while the smaller one enters the lower or anterior tentacles, dividing again in most species before doing so and sending a branch to the labial lobe. In *Succinea* the labial retractors are absent, but the lower tentacular retractor at the right side gives off a short stout muscle, which is attached to and acts as a subsidiary retractor to the penis-sheath.

FIG. 637.—Cephalic retractors of *Limax maximus* L., × 2, showing their common origin from the vestigial columellar muscle, and illustrating the section Monorhiza.

p. pharyngeal retractor ; *t*. tentacular retractors.

The pharyngeal or buccal retractor is the median muscle and passes through the nerve-ring, becoming attached at one or more points to the buccal bulb; it may, as in *Succinea*, be cleft to its base or, as is more usual, form a single strand which divides or merely dilates at its attachment to the buccal bulb.

The TRICHORHIZA (τριχῆ, in three parts; ῥίζα, a root) or species with three distinct proximal muscular attachments embrace *Testacella*, *Arion*, and certain *Hyalinia*. The muscle strands in those species possessing well developed shells, as *Hyalinia*, arise from the great columellar retractor, the pharyngeal muscle always having the most posterior origin upon it, differing in this respect from the group Monorhiza, in which it usually has a more anterior origin. In the *Arionidæ*, etc., the proximal terminations of the pharyngeal and tentacular retractors are affixed separately to the integument in the rear of the respiratory cavity, the pharyngeal retractor is

FIG. 638.—Cephalic retractors of *Arion subfuscus* Drap. × 3, illustrating the section Trichorhiza.

p. pharyngeal retractor ; *t*. tentacular retractors.

deeply cleft and arises to the right of the median line but posterior to the origin of the tentacular retractors.

Many differences in detail characterize the muscular arrangements of each group, *Testacella* in certain of its species developing a paired series of lateral muscles to the lingual sheath, which augment the contractile power of the terminal pharyngeal retractor, whose attachment has been transferred to the lingual sheath in correlation with its great development.

In the Pelecypoda the muscular system is strikingly symmetrical in accordance with their general organization, and consists chiefly of Adductors and Retractors, with other less important muscles having protractor or other functions.

The Adductors (*ad*, to; *duco*, I lead) are the very thick and powerful muscular pillars which connect together and close the valves of the shell of the Pelecypoda: they are considered to originate as modifications of the pallial musculature, and each muscle has its opposite ends attached to corresponding areas of the concave internal surfaces of the right and left valves, their places of attachment being shown by the more or less perceptible scars or impressions left thereon, which vary in size and distinctness according to the age of the animal.

The adductors have long been utilized for facilitating the classification of the Pelecypoda, and although their employment for this purpose is not now so fashionable as that of certain other organs of the body, yet if reasonable allowance be made for aberrant or specialized forms, and probably less allowance than required by other modes of arrangement, they remain as valuable and reliable for the purpose as any, furnishing also data for the phylogenetic history of the group and marshalling together the most nearly allied species.

According to the number and relative development of the adductors the Pelecypoda are divided into three groups : the Isomya or Dimya, the Heteromya, and Monomya.

The Isomya (ἴσος, equal ; μύς, muscle) is represented by *Anodonta* and other of our species, and possesses paired adductors approximately equal in size; the Heteromya (ἕτερος, different; μύς, muscle) to which group our *Dreissensia* belongs has two unequal muscles, the anterior one being in process of degeneration and often conspicuously smaller than the more centrally placed posterior one and tending to occupy a more and more anterior and less functionally important position in proportion to the enlargement and centraliza-

tion of the posterior adductor; while in the MONOMYA (μόνος, one; μύς, muscle) of which the Oyster is an example, the anterior adductor has become completely atrophied and lost, the enlarged posterior adductor assuming a more central position in the shell.

The adductors are distinguished as Anterior and Posterior, terms expressive of their relative positions in reference to that of the animal inhabitant.

The Anterior adductor is most dorsal in position and placed in front of and in constant association with the mouth, and is the first developed in the embryo, the more ventrally placed Posterior adductor being ventral to the rectum with which it is always in close relation appearing later, but their points of fixation to the shell gradually become more and more ventral in correlation with the growth of the shell, their bulk also correspondingly increasing, the newly-formed portion being generally distinguishable by its lighter colour.

FIG. 639.—Embryo of *Anodonta* seen from the left side, enlarged (after Götte), showing the early origin of the anterior adductor.
a.a. anterior adductor; *bl.* blastopore; *c.* ciliated area; *sh.* shell.

The adductors act by closing the valves of the shell, a portion of their substance being composed of involuntary or smooth muscle fibres, and the residue may be the pseudo-striate fibres characteristic of molluscan voluntary muscle; the valves, owing to the antagonistic action of the ligament, tend to remain slightly open when the muscles relax, this position being their state of rest or equilibrium.

The strength of the adductors is very great and, in certain cases, they have been known to resist a force many thousand times greater than the weight of the animal itself.

The RETRACTORS of the Pelecypoda are symmetrically arranged and paired muscles, strongly attached to corresponding areas of the concave inner surface of each valve of the shell, on which they leave permanent traces of their presence in the form of scars, the constituent fibres being distributed within the foot or other organs to which they may belong. In the archaic genus *Nucula*, the retractors emanate as usual from each valve and form an almost continuous series of muscular bundles between the adductors, but in more specialized forms they become concentrated, each muscle occupying a definitely circumscribed area of the shell surface.

In our Isomyate species the pedal retractors, which serve for the withdrawal of the foot, consist of two pairs of powerful muscles, affixed to the right and left valves at opposite ends of the shell, near to or continuous with the adductors, and distinguished as the Anterior or Posterior pedal retractors, according to the position they occupy. In some exotic Monomyate species, as *Pecten*, the right and left pedal

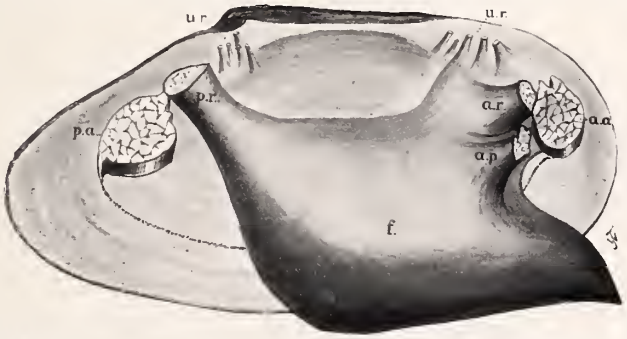


FIG. 640.—Left valve of *Anodonta cygnea* (L.), showing the position and character of the pedal musculature and the arrangement of the adductors characteristic of the Isomya.

a.a. anterior adductor; *p.a.* posterior adductor; *a.r.* anterior retractor of the foot; *p.r.* posterior retractor; *u.r.* umbonal retractors or pedal levators; *a.p.* anterior protractors; *f.* foot.

retractors are both affixed to the left valve and not equally distributed to both as is usual, or as in the byssiferous species the posterior retractors may, owing to the degeneracy of the foot, become transformed into the byssal retractors.

In *Dreissensia*, our only representative of Heteromya, the anterior pedal retractors are greatly attenuated and distally fixed to the umbonal region of the shell, the constituent fibres being distributed to the anterior base of the foot. The posterior retractors are correspondingly enlarged, attaining a comparatively enormous size, their position being indicated by an indistinct oblong scar of attachment near the superior margin of the valves and anterior to the scar of the posterior adductor; they have, however, become partially transformed into byssal retractors.

FIG. 641.—Left valve of *Dreissensia polymorpha* (Pallas), showing the muscular system characteristic of a byssiferous Heteromyan.

a.a. anterior adductor: *p.a.* posterior adductor; *a.r.* anterior pedal retractor; *p.r.* posterior pedal retractor, also functioning as retractor of the byssus.

The LOCOMOTION or progression of terrestrial testaceous Gastropods is more tedious and laborious than that of the aquatic forms, owing

to the weight of the body and shell being greater in air than in water.

Gastropods generally move with a true gliding motion, the foot-sole being continually adherent to the surface upon which they are crawling and not alternately loosened and re-applied thereto.

The locomotory muscles consists of longitudinal, transverse and obliqne fibres, closely interlaced with the somatic pedal musculature. The oblique contractile fibres shorten the foot and cause the lateral bending, the longitudinal fibres being extensile and constituting the true locomotory muscles; they are stimulated into activity by the action of the pedal ganglia and nerves, the intricate plexus of sympathetic pedal nerves which rhythmically continue the locomotory muscular action, creating a series of successive and distinctly perceptible waves of contraction and extension, flowing over the foot-sole from behind, forwards; and although the continuance of locomotory effort is governed by the rhythmical action of the sympathetic system, yet the rate of motion is manifestly shown to be under the control of the animal by their varying rates of progress and by the differing numbers of locomotory waves passing over the ventral surface of the foot. During the course of a brief summer evening's study of this feature, in a specimen of *Helix nemoralis*, at a temperature of 63° Fahr., I noted 50, 42, and 36 of these undulatory muscular waves per minute.

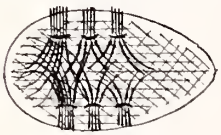


Fig. 642.

Fig. 643.

Schematic figures, showing the arrangement of the extensile locomotory muscles and of the variously distributed contractile fibres of the *Helix* foot (after Simroth).

Fig. 642.—Plan of the distribution of the muscular fibres as seen from above.

Fig. 643.—Diagram of the arrangement of the locomotory muscles as viewed laterally.

The rate of progression in Gastropods varies in accord with the environment, with the size of the animal and in correspondence with the shape and area of the locomotory disc, those species with long and narrow locomotory areas having greater powers of progression than those possessing a broad and short foot, and smaller species being relatively more active than those of larger size.

The Limaces, in which the locomotory muscular fibres are restricted to the median longitudinal third of the foot-sole, are the most active forms, travelling 13 to 14 centimetres per minute or at the rate of a mile in about eight days.

In the Helices and other terrestrial genera the locomotory disc presents a greater and more varied proportional area, and the rate of progress varies considerably in the different species, the smaller forms being relatively or even actually more nimble than the larger ones, *Helix cantiana* travelling 75 millimetres or more per minute upon a horizontal surface or at the rate of a mile in about 14 days 16 hours, a rate which is not exceeded by even *Helix aspersa*.

Cyclostoma elegans, to avoid or overcome the frictional resistance of close contact with the soil, while crawling, alternately raises from the ground and extends forward each lateral half of its longitudinally divided foot, seeking also to aid its progress by the accessory fixation of the snout, which is moistened by the secretion of special mucus glands, and yet it scarcely progresses 25 millimetres per minute, or at the rate of a mile in 44 days.

The aquatic branchiate species crawl upon the bed of the waters they inhabit or over and upon submerged objects, and although the greater density of water renders the weight of their shell less burthensome than it would be upon land, their average progress is but about 25 millimetres per minute or a mile in 44 days.

The Basommatophora, in addition to peregrinations upon the bed of the stream or pond, can by virtue of their greater buoyancy, due to the air within the respiratory cavity, float upon the surface and crawl with inverted shell upon the under side of the water-film by the successive undulations of the foot-sole as in the terrestrial species, these undulations being recorded by the transversely ridged mucous track left behind upon the surface of the water (fig. 607, p. 316); their progress is, however, aided by the strong vibratile cilia clothing the tentacles and the margins of the head and body and is stated to average 50 millimetres per minute or a mile in 22 days, although *Ancylus fluviatilis* has been recorded to travel only a little more than one millimetre per minute, or a mile in 2 years and 10 months.

Special observation at a temperature of 66° Fahr. showed that a moderate sized *Limnæa peregra* could crawl 75 millimetres per minute or a mile in 14 days 16 hours, while a half-grown *Planorbis corneus*, under similar conditions, accomplished 88 millimetres in the same space of time or a mile in 12 days 11 hours.

The Pelecypoda are very sluggish in their movements, the hatchet-shaped foot being more especially adapted for ploughing through sand and mud, and probably thereby disturbing the minute organisms

upon which they feed. In other cases the foot may be spread out laterally and form a disc.

Messrs. Boycott and Bowell have, however, recorded that the *Unio margaritifer* progresses 15 feet per day, or about 3 millimetres per minute, and a mile in 352 days.

The most sluggish of our species is the adult *Dreissensia*, which becomes fixed by its byssus to some suitable spot for considerable periods, this inactive adult life is compensated for by the activity of the young, which are free swimmers in their larval stage.

Within certain limits, snails can carry considerable weights without perceptibly impeding their rate of progress, showing that ordinarily they do not make full use of the strength they possess, certain Helices having been demonstrated to be able to travel on a horizontal surface with a weight fifty times their own, or ascend vertically, burthened with a weight nine times that of the weight of animal and shell combined. Mr. H. Crowther has also experimentally demonstrated that *Helix aspersa* can, even when loaded with a weight of 50 grammes (gramme = 15·432 grains) ascend a vertical glass plate at a speed of seven millimetres per minute, but when the weight was increased to 68·9 grammes, the animal though able to raise the load, could not progress; while *Helix arbustorum*, whose foot area is barely eight inches, has, under the same conditions, ascended at a similar speed with a weight of $8\frac{1}{4}$ grammes, but a weight of $8\frac{3}{4}$ grammes was beyond its strength, as the animal was quite unable to raise the burthen and slipped off the glass.

The Reproductive or Sexual System in the mollusca is very varied in the character and complexity of its component parts, the simpler the organization the fewer the sexual characters exhibited, while sexual differentiation is naturally most pronounced in the most highly organized types, and although all organisms tend to vary in an infinite variety of ways, the different organs are not equally affected nor do they undergo modifications in a similar way nor in an equal degree.

The sexual organs at ordinary times are only normally of moderate bulk, but at the approach of the pairing season they become turgid and increase vastly in size, often occupying the greater part of the body cavity. This pairing season is not the same for all species, but spring is perhaps the most favoured season, the reproductive organs at that period being pre-eminently noteworthy for the great abun-

dance of large glycogen-bearing plasma shells by which they are so densely enveloped, this feature being most strikingly displayed by their accumulation among and around the constituent follicles of the germ glands; their presence being clearly concerned in the provisioning and maturation of the ova and spermatozoa, as the store around the germ glands and sexual organs generally becomes exhausted during the reproductive season.

Although reproductive power is usually associated with the attainment of full growth, it is well established that sexual maturity, with power to perpetuate their kind, is often fully acquired by individuals whose shells are far from being completely grown and therefore quite destitute of the usual adult characters.

The male organs frequently mature somewhat in advance of those of the female, constituting PROTERANDRY (πρώτος, first; ἄνηρ, male) or more rarely, as in *Agriolimax lævis*, may exhibit PROTEROGYNY πρῶτος, first; γυνή, female), the female organs first acquiring functional perfection. In many of the Stylommatophora, however, Prof. Babor has verified that the genital organs almost invariably undergo a series of successive metamorphoses, in which the animals are first functionally unisexual and only subsequently become hermaphrodite; this condition, however, is not always the termination of their sexual development, as the same animal may again become unisexual, by the atrophy of the sexual organs first developed and the retention of those acquired later.

In accordance with their sexual characteristics, the mollusca fall naturally into two great groups, Diœcia and Monœcia.

The DIŒCIA (δύω, two; οἶκος, house) or Unisexual species comprise the great majority of the mollusca, and include all the Chitons and Cephalopods, and nearly all Pelecypods and Streptoneura.

This group is especially composed of the simply organized or primitive species and of certain of the more active and highly specialized groups, the sexual organs being often so simple and undifferentiated, and so similar in the two sexes as to be undistinguishable except by microscopic examination, often consisting merely of a genital gland or glands, composed of ramified aggregations of cœca of simple structure, and a duct or ducts leading therefrom and opening within the exhalent chamber in the Pelecypoda or directly to the exterior immediately behind and near to the anus in the Aphalliate Gastropoda.

These genital ducts may be special, or the nephridial ducts may be utilized, the genital products falling into the kidneys direct or by way of the pericardium and thence conveyed to the exterior.

The Diœcia for convenience of study may be classified as Aphallia, Exophallia, and Cryptophallia.

The APHALLIA (*α*, not; *φαλλος*, penis) are characterized by the absence of any organ by which copulation can be accomplished, the reproductive organs simply consisting of a paired ovary or testis, and the ducts leading therefrom to the exterior, no accessory organs are developed, the Spermatozoa being simply shed by the male into the circumambient water and some making their way to the ova or to the oviducal tract of the female; this organization is possessed by all the Diœcious Pelecypoda, the Chitonidæ, and many of the more archaic Diotocardiate Gastropods. There is little sexual dimorphism displayed, but the female of *Unio tumidus* is said to develop a broader shell than that of the male.

The EXOPHALLIA (*ἔξο*, external; *φαλλος*, penis) embrace those diœcious species in which the males have acquired an external copulatory organ, projecting freely from the right side of the neck and arising as a muscular outgrowth from the body-wall; it may be as a dependence of the head as in *Vivipara*, etc., of the mantle as in *Ampullaria*, or of the foot as in the generality of species. It is strongly erectile and extensile by concentrated blood pressure, and though not eversible and retractile as in the Cryptophallia, it can often be bent in a sigmoid form and hidden beneath the mantle folds, the spermatozoa being conveyed thereto, in the more primitive forms, in which the male organ is a solid and thick appendage, by an open ciliated duct; in more highly organized forms this duct becomes closed and included within the body, and constitutes the

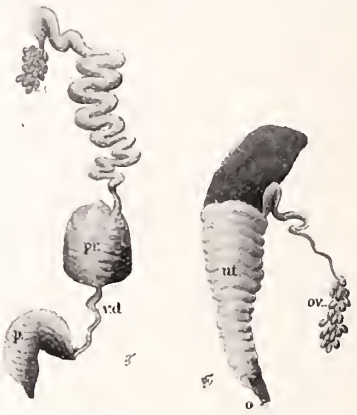


FIG. 644. FIG. 645.

FIG. 644.—Male reproductive organs of *Cyclostoma elegans* (Müll.), × 3, illustrating the organization of the Diœciate Exophallia.

p. penis; *v.d.* vas deferens; *t.* testis; *pr.* prostate.

FIG. 645. — Female reproductive organs of *Cyclostoma elegans* (Müll.), × 3 (the indistinct and only partially separated spermatheca is not shown).

ov. ovary; *ut.* sacculated or glandular oviduct; *v.* vagina; *o.* female orifice.

vas deferens, which may widen into a seminal glandular vesicle or prostate in some part of its course.

The female organs develop an albumen gland, a glandular sacculate oviduct and a more or less definite spermatheca or vesicle to receive the fertilizing spermatozoa. All our diœcious Streptoneures, except *Neritina* and *Vivipara*, are exophalliate, *Cyclostoma*, *Bithynia*, etc., being examples. There is also sometimes a certain degree of external sexual dimorphism, the male possessing a slenderer form and a permanently projecting male organ, and the female being larger and relatively more turgid. In some genera this dimorphism is variously displayed, by *Littorina* at the mouth of the shell, by *Cerithium* in the operculum, by *Nassa* in the radula, etc.

The Cryptophallia (κρυπτός, hidden; φαλλος, penis) are in the Diœcia restricted in this country to *Neritina fluviatilis*, in which the male copulatory organ is stated to be retractile within a penis sheath capable of withdrawal into the body cavity, as in the Pulmonata, although *Vivipara* may also be regarded as belonging to this group, as the contractile male organ is concealed within the right tentacle, which is sensibly deformed thereby.

The general character of the organization of the diœcious Cryptophalliate Gastropods is not, however, sensibly divergent from the usual diœcious type, and only differs from the Exophallia by the retractibility of the male organ, although the vas deferens is of an enormous length, the prostatic portion of its course being combined into a large compact mass upon the penis sheath, a similar concentration of the prostate, however, exists in *Vivipara*, *Cyclostoma*, and even in *Succinea*.

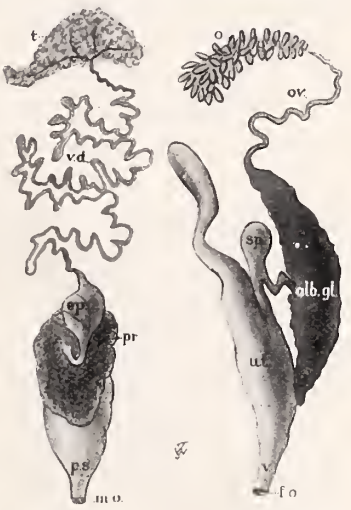


Fig. 646. Fig. 647.

Fig. 646.—Male reproductive organs of *Neritina fluviatilis* (L.), × 4 (after Moquin-Tandon), illustrating the Diœciate Cryptophallia.

t. testis; *v.d.* vas deferens or sperm duct with enlarged sperm vesicle or epididymis *ep.*; *pr.* prostate; *p.s.* penis sheath; *m.o.* male orifice.

Fig. 647.—Female reproductive organs of *Neritina fluviatilis* (L.), × 4 (after Moquin-Tandon).

o. ovary; *ov.* oviduct; *alb. gl.* albumen gland; *sp.* spermatheca; *ut.* uterus or matrix; *v.* vagina; *f.o.* female orifice.

The MONŒCIA (μόνος, one; οἶκος, house) in which group both sexes are combined in the same individual, is in its lowest forms, except in this respect, very little different from the Diœcia; still in addition to the combination of both sets of organs, the group generally shows greater specialization and a remarkable development of accessory sexual organs. Hermaphroditism, according to Pelseneer, appears to be due to the grafting or superposition of the male system upon that of the female, and to have been apparently influenced in this direction by the adoption of terrestrial or fluviatile habits or parasitism.

The increased bulk and complexity of the sexual organization, owing to the combination of the male and female organs within the body of each individual and the number of highly differentiated accessories that have been developed, is so marked that the greater part of the body cavity is occupied by them, especially during the pairing season, when they appear to dominate the whole organism.

Yet, although both sexes are thus combined in each individual, the hermaphroditism is not complete, as conjugation with a second individual is normally always essential to ensure the fertilization of the ova and the development of the offspring.

For the purposes of study, the Monœcia, like the Diœcia, may be separated into three chief groups: Aphallia, Exophallia, and Cryptophallia.

The APHALLIA (α, not; φαλλος, penis) are restricted to the Pelecypoda in general, and include a few genera more especially fluviatile in habit, as *Sphærium*, *Pisidium*, and certain species of *Unionidæ*; they, however, differ little from the Aphalliate Diœcia, excepting that both the sexual elements are developed within the same individual, though the male and female gonads may occupy, as in the *Sphæriidæ*, separate regions of the body, but as the ova and sperm are not usually developed simultaneously, the difficulty of appreciating their peculiarities is considerably increased especially when but one excretory duct is present.

The EXOPHALLIA (ἔξο, external; φαλλος, penis) are also closely similar to their Exophalliate Diœcious kindred, except for the combination of male and female sexual organs within the body cavity of each individual, and the increase in number and complication of the supplementary organs. The Monœciate Exophallia are few in number, our only representatives being the species of the genus *Valvata*, in which group a primitive simplicity of general organization persists in spite of the acquirement of the hermaphrodite sexual

combination, shown by the retention of the permanently projecting male copulatory organ, distinguishing other Streptoneures, *Valvata* not having acquired the retractile penis characteristic of most hermaphrodite species.

The CRYPTOPHALLIA (κρυπτός, hidden; φαλλος, penis) are characterized by the possession of a male conjugatory organ, which is surrounded or enclosed by a protecting sheath completely retractile within the body cavity, and also exhibiting a great accession and complexity of accessory organs.

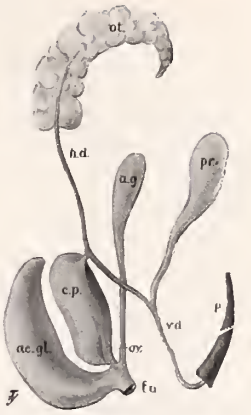


FIG. 648.—Reproductive organs of *Valvata piscinalis* (Müll.), ×4 (after Bernard), illustrating the Monœciate Exophallia.

ot. ovotestis; *h.d.* hermaphrodite duct; *pr.* prostate; *v.d.* vas deferens; *p.* penis; *ov.* oviduct; *c.p.* copulatory pouch or spermatheca, the uterus of Pelseneer; *a.g.* albumen gland, the spermatheca of Pelseneer; *ac.gl.* accessory shell gland, the albumen gland of Pelseneer; *f.o.* female orifice.

The Cryptophallia in accordance with the separation or combination of the apertures of the male and female system of organs, may be subdivided into two groups: Ditremata and Monotremata.

The DITREMATA (δύω, two; τρῆμα, cavity) comprise the *Limnæidæ* and *Carychiidæ* and are characterized by the marked separation of the male and female orifices; the male aperture is placed beneath the tentacle upon the right side of the neck in the dextral species, and on the left side in those sinistrally coiled; the female aperture being situated beneath the mantle-flap in the pallial region on the same side of the body but comparatively remote from the male aperture.

This position of the female genital aperture is a survival of the archaic arrangement found in some of the Diotocardia in which

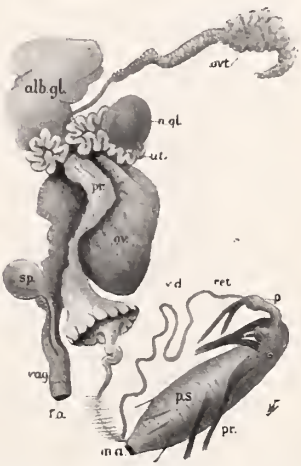


FIG. 649.—Reproductive organs of *Limnæa stagnalis* (L.), ×2, illustrating the Monœciate Ditremata.

ovt. ovotestis; *pr.* prostate; *v.d.* vas deferens; *p.* penis; *ret.* penis retractors; *p.s.* penis sheath with its protractors *pr.*; *m.a.* inale aperture; *alb.gl.* albumen gland; *n.gl.* nidamental gland; *ut.* uterus; *ov.* oviduct; *sp.* spermatheca; *vag.* vagina; *f.o.* female orifice.

the sexual products of both sexes are expelled by ducts opening from the pallial region, a position still retained by the female aperture in this group. There is also a greater complexity and differentiation of the albuminous glandular part of the female system, probably in correlation with the albuminous mass within which the eggs of the *Limnœidæ* are deposited.

The MONOTREMATA (μόνος, single ; τρῆμα, cavity) embrace those hermaphrodite species in which both male and female organs open exteriorly by a common aperture; they exhibit the highest organization attained by the sexual organs in the species within the sphere of our studies acquiring a greater complexity and wealth of accessory organs. The external aperture, though common to both series of organs, yet during extrusion exhibits a terminal female opening and a masculine lateral one.

For convenience of study the Monotremata may be separated into three groups : Haplogama, Gynogama, and Belogama.

The HAPLOGAMA (ἁπλοῦς, simple; γάμος, marriage) are the most simply organized of the Monotremata, establishing them as regards their genitalia to be the most ancient type; their organization comprising on the male side the ovotestis, the hermaphrodite duct which ends in a cœcum at the base of the ample albumen gland, the prostatic tract which is adherent to the glandular oviduct, but later becomes free as the vas deferens, and joining the penis which is enclosed by a sheath, to which a retractor muscle is affixed. The female organs embrace the ovotestis, the oviduct, and the vagina, where the spermatheca usually opens.

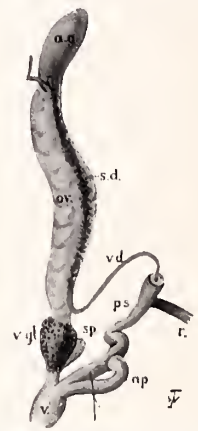


FIG. 650.—Reproductive organs of *Zua lubrica* (Müll.), ×12 (after Ihering), illustrating the Cryptophalliate Haplogama.
s.d. sperm duct ; *v.d.* vas deferens ; *p.s.* penis sheath ; *r.* retractor muscle ; *ap.* appendix ; *a.g.* albumen gland ; *ov.* glandular oviduct ; *sp.* spermatheca ; *v.* vestibule ; *v.gl.* vaginal gland.

Except for the presence of an appendix as an adjunct to the penis in certain species, and which may possibly be a relic of a primitive flagellum, such as is still persistent in *Bithynia* and other groups, and of a so-called appendicula on the female side, there are no accessory organs such as those developed in the Stylogama.

The GYNOGAMA (*γυνή*, female; *γάμος*, marriage) are confined in this country to the *Arionidæ*, and are particularly characterized by the atrophy and loss of the male intromittent organ, and the transfer of its function and retractor muscles to the vagina and spermatheca which usurp its function and are everted during copulation, the male portion being merely the amplified sperm duct or epiphallus which moulds the spermatozoa in the form of a spermatophore for transference to the copulatory pouch of its mate. The atrium or vestibule which opens beneath the pulmonary orifice on the right side of the body is enveloped by a dense glandular pad which may represent the digitate glands of the Stylogama.

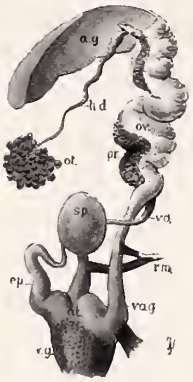


FIG. 651. — Reproductive organs of *Arion hortensis* Fér., × 2, illustrating the Cryptophalliate Gynogama.

ot. ovotestis; *h.d.* hermaphrodite duct; *pr.* prostate; *v.d.* vas deferens; *ep.* epiphallus; *a.g.* albumen gland; *ov.* sacculated or glandular oviduct; *sp.* spermatheca; *vag.* vagina; *at.* atrium; *v.g.* vestibular gland; *r.m.* retractor muscles attached to spermatheca and vagina.

The STYLOGAMA (*στῦλος*, a rod; *γάμος*, marriage) are the most complexly organized of the Monotremata, often developing a number of highly differentiated organs in connection with the reproductive function.

The female organs possess highly specialized vaginal prostates or vesiculæ multifidæ in the form of ramified digitate glands, which are usually paired and placed at each side of the vagina, into which they open; the number of these glandular digitations varies greatly in the different species, or even in the same species; there may be few or, as in *Helix pomatia*, they may, though varying greatly individually reach thirty or forty digitations to each gland.

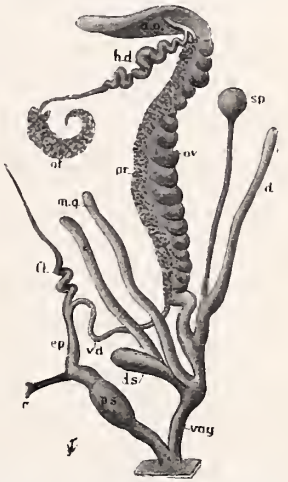


FIG. 652.—Reproductive organs of *Helix lapicida* L., × 2, illustrating the Cryptophalliate Stylogama.

ot. ovotestis; *h.d.* hermaphrodite duct; *pr.* prostate; *v.d.* vas deferens; *fl.* flagellum; *ep.* epiphallus; *p.s.* penis sheath; *r.* penial retractor; *ov.* sacculate oviduct; *sp.* spermatheca; *d.* its diverticulum; *m.g.* digitate mucus glands; *d.s.* dart sac; *vag.* vagina.

Near to the vaginal apertures of the digitate glands is the opening of the Stylophore, or dart sac, which commonly consists of an ovoid muscular sac within which is secreted a pointed calcareous spiculum used in the preludes leading up to sexual conjugation.

The spermatheca or copulatory pouch often develops an additional and more capacious diverticulum, which may attain a considerable length, and usually receives the spermatophore transferred during copulation.

The male organs are chiefly augmented by the development of the flagellum, a blind glandular diverticulum at the distal end of the penis sheath, within which or in an intermediate epiphallial tract the spermatophore is moulded; these spermatophoral tracts may be separated from the penis sheath by a strong and outwardly visible sphincter muscle, or the separation may be less distinct.

The Reproductive System of the Diœciate species have fewer constituent parts than the gastropodous Monœcia, in which a variety of auxiliary organs have been developed, supplementing or more perfectly discharging the necessary functions in connection with reproduction.

The Gonads (γονος, seed) or germinal glands, the essential organs of the sexual system, are paired and symmetrical in the Pelecypoda but single in the Gastropoda. These organs possess a structureless outer wall, the internal germinal epithelium being composed of rounded cells, and derived from the walls of the cœlomic or secondary body cavity of which they form a more or less definite part.

In the Diœciate Gastropods and Pelecypods there are male gonads or testes, producing only spermatozoa or zoosperms, and female gonads or ovaries, producing eggs only, but in the ovotestis of the Monœciate or hermaphrodite species both eggs and spermatozoa may

Fig. 653.

Fig. 654.

Fig. 653.—Ovotestis of *Limnæa peregra* (Müll.), × 3, showing its lobulated arrangement.
Fig. 654.—Ovotestis of *Helix aspersa* Müll., × 3, showing its sometimes tufted character.

be produced by the same gland, although in the hermaphrodite Pelecypods *Sphærium*, *Pisidium*, etc., the male and female gonads are separated in two regions, an anterior male region and a female more posterior one, with, however, a common efferent duct.

In the Gastropoda, the richly lobed and convergent diverticula forming the gland vary greatly in their compactness and general

aspect and arrangement, and usually lie within the body cavity, between the lobes of the digestive gland, with which its parts may be intimately intermingled. In the Pelecypoda the paired gonads are usually richly branched tubular or lobate masses, often occupying the base of the visceral mass and permeating amongst the intestinal coils.

The Hermaphrodite Duct (*Ἑρμῆς*, Mercury; *Ἀφροδίτη*, Venus) the conjoint canal of the ova and semen, is only found in the monœcious species, originating at the ovotestis or hermaphrodite gland, and terminating in the seminal vesicle at the base of the albumen gland; its swollen part is the epididymis of continental authors, but the duct is very variable in its character and extent, it may be voluminous, sinuously convoluted and deeply pigmented as in *Succinea*, simple and nearly straight as in *Hyalinia*, or beset with numerous glandules along the greater part of its course as in many of the *Limnæidæ*.

The Seminal Vesicle (*semen*, seed; *vesicula*, dim. of *vesica*, a bladder) or Claw, known also as the Epididymic cœcum, is a variously formed cœcal diverticulum, situate at the base of the concave side of the albumen gland, to which it is closely apposed; it is sometimes constituted by a mere swollen convolute termination of the hermaphrodite duct, or, as in *Succinea*, may be paired, and open with the albumen gland into a fertilizing cavity, but in some species beneath the point where the swollen portion is imbedded in the albumen gland there is a lateral tube bearing several blind ramifying tubules lined with ciliate ungranulated epithelium, which is lodged between the ascending and the swollen descending part of the efferent canal and in the adult contain living spermatozoa which fertilize the ova before passing within the sacculated and glandular oviduct.

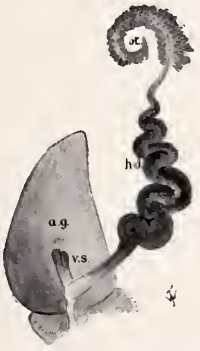


Fig. 655.—*Succinea elegans* Risso, ×6, showing the character and relationship of the pigmented hermaphrodite duct, the paired seminal vesicles, the albumen gland, and the ovotestis.

a.g. albumen gland; *h.d.* hermaphrodite duct; *ot.* ovotestis; *v.s.* seminal vesicles.

The Albumen Gland (*album*, white) is an adjunct of the female system, and is a light-coloured linguiform organ, convex behind and concave in front, where the hermaphrodite duct terminates in the seminal vesicle. The gland is very slightly adherent to the

first part of the ovispermatoduct which may be hollowed for its reception and with which it communicates. It varies in size, not only according to the species but periodically, being very voluminous at the pairing season, when it plentifully secretes a viscid albuminous fluid containing globules and granular matter with which the descending ova become surrounded.

The Sperm Duct (σπέρμα, seed) in the dicœcious species originates at the testis or male gonad, it is often of considerable length and may follow a tortuous course, usually becoming differentiated as a prostatic glandular enlargement in some part of its course before reaching the male organ.

Fig. 653.—Section through the prostatic portion of sperm duct of *Limnæa peregra* (Müll.), ×10, showing its glandular character.

In the monœcious species there is a combined conduit or hermaphrodite duct which conveys both ova and sperm, the two becoming separated at the seminal vesicle, the ova following the oviduct, and receiving their store of albumen, etc., and the zoosperms passing down the conjoint sperm duct which is attached to the concave side of the oviduct and beset with glandular follicles, forming a prostate, which becomes greatly swollen at pairing times; the separation between the oviduct and sperm duct may be incomplete, as in *Arion*, in which the two channels communicate along their whole combined course.

The Vas Deferens (*vas*, a vessel; *defero*, to carry away) is the sperm conduit when freed from adherence to the oviduct and before its arrival at the male organ; on its course it may develop a seminal sac, as in *Limnæa*, or become enlarged near its termination, and secrete the spermatophore, as in *Hyalinia*. In some of the primitive Exophalliate Gastropods the sperm duct terminates externally in the pallial region as in the Aphalliate species, but in correlation with the development of an external copulatory organ, an open ciliated conduit became established, leading along the side of the body from the pallial termination of the sperm duct to the apex of the intromittent male organ; this open duct became gradually enclosed within the body, and now constitutes the vas deferens, a certain section of its course even yet, however, retaining an intermuscular course beneath

Fig. 657.—Open ciliated external sperm-duct of *Pelta coronata* (highly magnified), (after Pelseneer).
s.f. seminal furrow; *m.* mantle; *f.* foot.

the integument. The primitive external spermatic groove present in the ancestors of the Pulmonates, and still persisting in some Opisthobranchs, has left indication of its former presence and external position in the lateral or genital groove connecting the pallial opening with the reproductive orifice which is still found in so many species.

The Flagellum (*flagellum*, a whip-lash) is the blind diverticulum often found in highly organized Gastropods as a prolongation of the epiphallus or of the distal end of the penis-sheath, wherein is secreted

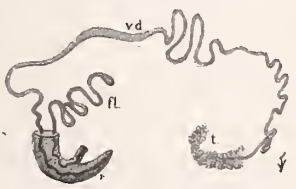


Fig. 658.—Male reproductive system of *Bithynia tentaculata* (L.), × 6, showing the semi-independent flagellum.

t. testis; *v.d.* vas deferens terminating at the apex of penis; *fl.* flagellum, opening in a separate but subsidiary prominence thereon.

a sheath or case for the safer transfer of the seminal element to the partner. It is very variously shaped, externally and internally, and the spermatophore moulded within it is an exact reproduction or cast of the shape and denticulations of the interior of the cœcum.

In *Bithynia* and certain species of Streptoneura, as well as in *Ancylus*, the flagellum opens to the exterior more or less independently of the penial orifice of the sperm duct, the orifice of the flagellum in *Bithynia* being upon a subsidiary but distinct bilobation of the penis; an intermediate but interesting modification of this form of flagellum is found in *Buliminus* and *Pupa*, in which the flagellum does not form a continuation of the distal end of the penis-sheath as in *Helix*, etc., but opens into the common vestibule or into the lower part of the penis sheath, and it would appear not improbable that the appendix to the penis-sheath of certain Gastropods is homologous with this organ.

Fig. 659.— Reproductive organs of *Buliminus montanus* (Drap.), × 3, showing the epiphallus and also the flagellum subsidiary to but proximally connected with the penis.

a.g. albumen gland; *ot.* ovotestis *h.d.* hermaphrodite duct; *ov.* oviduct; *v.* vagina; *fl.* flagellum; *v.d.* vas deferens; *ep.* epiphallus; *p.s.* penis sheath; *r.* retractor; *sp.* spermatheca and branch.

The Epiphallus (επι, upon; φαλλος, penis) or Patronenstrecke, is merely an enlargement of the anterior end of the vas deferens, and includes the tract between the outlet of the vas deferens and penis, and has not usually a retractor muscle, nor is it evertible.

Its function in common with the flagellum is merely to accumulate and agglutinate the spermatozoa together or enclose them within a firm chitinous sheath or spermatophore which varies in its shape according to the species.

The Penis (*penis*, a tail) is the masculine intromittent organ, and is only developed in our fauna amongst the Gastropoda, always occupying the right side of the anterior part of the body in dextrally organized individuals.

In the Streptoneura it is a permanently external outgrowth from the body-wall, and may be a dorsal development as in *Cyclostoma*, with innervation by the sub-intestinal ganglion, a cephalic organ as in *Vivipara*, a pedal organ as in *Valvata*, or a pallial organ as in the exotic *Ampullaria*, their character being indicated by their innervation.

The penis sheath to which the vas deferens conducts the spermatic fluid encloses the male intromittent organ, which occupies the distal end of the sac, and may be separated from the flagellum or epiphallial tract by a constricting muscular annulus. The sheath is usually a large somewhat fusiform or clavate sac, but assumes a great variety

Fig. 660.

Fig. 661.

Fig 662

Fig. 660.—*Valvata piscinalis* (Müll.), × 2, showing the permanently projecting male organ.

Fig. 661.—Penis sheath of *Helix rufescens* Penn., opened to show the male intromittent organ, × 12.

Fig. 662.—Penis sheath of *Limnæa palustris* (Müll.), × 10, opened after pairing before complete retraction, showing how the sac becomes the intromittent organ by eversion.

p. penis ; *p.s.* penis sheath ; *v.d.* vas deferens ; *r.* retractor muscle ; *m.m.* longitudinal muscular pillars, possibly protractors and guides.

of shapes, and furnishes important characters utilized in classification and in the differentiation of species, affording in the *Succineæ* a ready means of separation between the doubtful intermediate specimens connecting *Succinea putris* and *S. elegans*.

From the naked and permanently external organ of the Streptoneures, many lines of variation have arisen, leading to the form concealed within an ample sheath or sac and capable of retraction or protrusion through the genital orifice, a form especially characteristic of the Euthyneura; or the typical intromittent organ may itself become atrophied and its function be performed by the inversion of the penis sheath as in many *Limnæa*, while in the *Arionidæ* the sheath also becomes lost, the epiphallus opening directly into the genital vestibule, and the intromittent function being relegated to the vagina and spermatheca duct.

In *Helix acuta* the penis sheath contains a perforate calcareous body to which the epiphallus and retractor are fixed. Our *Zonitoides* present a similar feature formed, however, by the apposition of two calcareous but somewhat dissimilar hollowed or channeled plates.

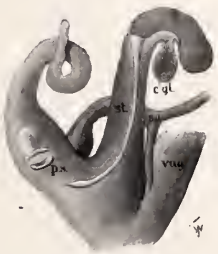


FIG. 663. — Proximal portion of sexual organs of *Zonitoides excavata* (Bean), × 10, (from a photograph by Mr. W. Moss), showing the position and character of the calcareous penial plates and the organization generally.

st. stylophore or dart sac, showing natural position of dart and character and position of the coronal gland, *c.gl.*; *p.s.* penis sheath with calcareous channeled plates; *vag.* vagina; *sp.* bifid spermatheca duct.

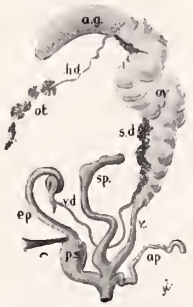


FIG. 664. — Reproductive organs of *Helix acuta* Müll., × 2, more especially to show the position and character of the appendix.

a.g. albumen gland; *ot.* ovotestis; *h.d.* hermaphrodite duct; *ov.* oviduct; *v.* vagina; *s.d.* sperm duct; *v.d.* vas deferens; *ep.* epiphallus; *p.s.* penis sheath with retractor; *sp.* spermatheca.

The APPENDIX is an external adjunct to the reproductive system, opening into or near to the penis sheath; its function is uncertain, but I do not regard it as improbable that its affinities are with the semi-independent flagellum found in *Bithynia, Buliminus*, etc., and other groups which have a similar position in relation to the penis.

The UTERUS or GLANDULAR OVIDUCT is the convolute and spacious duct with sacculate glandular walls through which the ova pass after fertilization, becoming well developed and surrounded by the secretion of its walls. In the hermaphrodite species it is more or less intimately united with the prostate or glandular sperm duct, from

which it separates as the vagina, the sperm duct becoming the vas deferens.

The VAGINA (*vagina*, a sheath) is the oviduct when freed from its adherence to the glandular sperm duct; it then becomes more muscular and contracted, and several auxiliary organs open into it, the uppermost being the vaginal glands; these may exist as a dense investment surrounding the vagina, or in the more advanced forms take the shape of a variable number of digitate or finger-shaped tubes, which are usually paired and placed at either side of the vaginal tube.

FIG. 665.—Proximal portion of reproductive organs of *Hyalinia alliaria* (Miller), × 6, showing the position and character of the vaginal glands.
ov. oviduct; *v.gl.* vaginal glands; *s.d.* sperm duct; *v.d.* vas deferens; *p.s.* penis sheath; *sp.* spermatheca.

FIG. 666.—Proximal portion of reproductive organs of *Helix rufescens* Penn., × 6, showing the character and arrangement of the paired digitate vaginal glands.
v.gl. vaginal glands; *v.* vagina with dart sacs; *p.s.* penis sheath.

The vaginal glands discharge directly into the vaginal tract, or in the case of the digitate glands may retain their secretions and discharge the secreted contents as required.

The APPENDICULA is an outgrowth of the female system, whose particular function is as yet unknown, but it has been assumed to act as a receptacle for spermatophores.

The EGERSIDIA (εγερσις, an exciting, an awakening) are possessed in various forms by widely different groups of mollusks and are special organs whose function is to stimulate or excite sexual passion or desire and thus include not only the fleshy "reizkörper" of the *Limacidæ* and the fully calcareous or chitinous love-darts of the Helices and other genera, but any organ by whose actions amorous feelings are encouraged.

Although so different in aspect and structure, the calcareous love-dart and the fleshy reizkörper are equally and simply excitatory organs, and numerous intermediate forms exist linking them together, all subserving the same purpose of producing or increasing the amorous desire leading up to sexual congress, as the egersidia in their

typical form take no part in the true coupling, serving only as their name implies to provoke that act.

Excitatory functions are not, however, a trait restricted to either sex, as stimulatory adjuncts to both the male and female organs have been demonstrated to exist, and it is probable that most mollusks are provided with special stimulatory organs or possess some other means of allurement or attraction to sexual union.

According to their character the excitatory organs may be grouped under the two heads, Sarcobela and Gypsobela.

The SARCOBELUM (σαργο, flesh; βέλος, an arrow) or excitatory organ, the "reizkörper" of the Germans, "organ excitateur" of the French, is usually a soft and fleshy linguiform eversible process, erectile by blood pressure, and occasionally furnished with a harder calcareous point with which each animal strokes, pats, and caresses its prospective partner during their amorous preludes. This organ is usually located within the genital passage, near the outlet, and may be cleft at the base for the passage of the copulatory organs.

FIG. 667.—Spermatheca duct of *Zua lubrica* (Mull.), × 30, laid open to show position and character of the sarcobelum or excitatory organ (after Ihering).

Unlike the Gypsobelum, which is more particularly an adjunct to the female system, the Sarcobelum is more especially, though not exclusively, a masculine excitatory organ, and is usually present in the form of an erectile muscular appendage within the penis sheath, as exemplified in *Agriolimax agrestis* and other species, but similar alluring developments exist within the atrium of other species, occupying an intermediate position between the two groups of organs in the hermaphrodite species and not strictly supplementary to the organs of either sex, or these stimulating appliances may, as in *Amalia*, be slightly within the vagina or other feminine duct, and really appertain to the female system.

FIG. 668.—*Agriolimax agrestis* (L.), with its sarcobelous excitatory organ protruding.

In the Diœcious *Viviparidæ* we find a probable prototype of the Egersidium in the erectile fleshy appendage upon the inner walls of the vaginal tube, which may be regarded as a primitive Clitoris or

feminine excitatory organ, perhaps derived from some earlier form from which originated the diversely constituted egersidia of the various genera.

Fig. 669.—Terminal part of male organ of *Planorbis corneus* (L.), greatly enlarged (after Moquin-Tandon), showing the vibratile stimulatory appendage.

Stimulatory functions are, however, not strictly confined to special egersidia, as the male organ may itself bear at its apex a vibratile appendage whose function is probably of an excitatory character.

The Gypsobelum (γύψον, lime; βέλος, an arrow), love-dart, or Spiculum amoris, is essentially a feminine stimulatory organ, and is a slightly flexible, straight, curved, or even slightly twisted glistening-white weapon, formed principally of carbonate of lime, and becoming fragile and brittle when dry; its free end terminates in a fine point, and the enlarged base fits upon a conical tubercle at the bottom of the dart-sac.

The dart is formed very rapidly, the process usually occupying less than a week; the shaft first appears as a slender spicule attached to the apex of the tubercle, increasing simultaneously in length and breadth, the blades which are moulded by the walls of the sac being next formed, the conical base and annulus being the last to be finished, these are sometimes composed of numerous longitudinal calcareous rods, resembling a cricketer's leg-guard, and crenulate at top and bottom, the tubercle having corresponding sulci, and projecting into the expanded base of the dart.

Fig. 670.—Annulus of dart of *Helix aspersa* Müll., × 3, with adherent viscous secretion as left after the loss of the dart.

The mode of usage of the dart does not yet seem to be universally known; the old writers considered it to be a missile hurled by one snail at another, and this mode is still spoken of by some modern writers, as though the dart was launched through the air and buried in the tissues of the companion snail. The dart is fitted upon the tubercle, attachment being assisted by a viscid secretion which extends within the hollow shaft of the dart itself, the dart being exserted for use by the eversion

Fig. 671.—Partial dissection of *Helix aspersa* Müll., showing portions of love-darts of previous partners which have become lodged in the viscera.

of the dart-sac, its exposed point being pressed against and slightly piercing the body of the companion snail.

Owing to the slight attachment to the tubercle the dart may be lost during use, and fall to the ground, or become adherent to the exserted organs, and be afterwards withdrawn with them into the body, working its way amongst the organs, and eventually becoming lodged in the viscera, as many as three darts have been found thus lodged in the interior of the body of a single animal.

Great variation in form of the love-darts exists amongst even the few teliferous British species, and a scale or series of forms from simple to complex may easily be constructed, showing the gradual modifications leading from one type of dart to another, but a start-

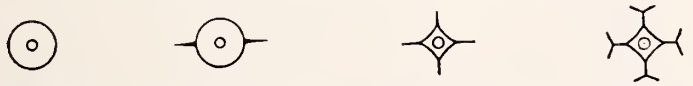


FIG. 672. FIG. 673. FIG. 674. FIG. 675.

Magnified diagrammatic sections of darts of certain species of British teliferous Gastropods, showing the gradation from a simple to a complex structure.

FIG. 672. *Helix hispida* L. FIG. 673. *Helix itala* L.
FIG. 674. *Helix aspersa* Müll. FIG. 675. *Helix pisana* Müll.

lingly close affinity in the shape and general character of the dart is exhibited by species distinctly different in general aspect, thus *Helix lapicida* and *Helix arbustorum* have practically identical darts, those of *Helix aspersa* and *Helix nemoralis* possess the same peculiarities, and there are other remarkable approximations in the aspect of the darts the animals of which, judged by their shells alone, are not very intimately related.

Equally striking is the remarkably different darts sometimes possessed by closely allied species, those of *Helix nemoralis* and *Helix hortensis* being so remarkably distinct that doubtful intermediate forms of these species can only be settled with absolute certainty by their aid.

Schmidt affirms a correlation between the character of the dart and the number of bands present upon the shell, those species with a pyramidal subulate dart and mucous glands of more than eight cœca have normally not more than five bands; those species, like *Helix arbustorum*, with a lanceolate dart and two simple or bifid mucous glands, have never more than four, while two subulate curved darts are associated with numerous spirally arranged linear markings upon the shell.

Darts may be found within the dart-sac at all times of the year, but some species are much more liable than others to lose them, and if lost just prior to hibernation, it is probable that their renewal will be delayed until spring, but in *Trichotoxon*, an exotic genus of slugs, the darts are permanent and are even furnished with chitinous sheaths.

The Gypsobela or love-darts, according to the greater or lesser modifications they display, may for purposes of study be conveniently grouped in four sections, based upon the degree of complexity attained by the supporting lateral blades, viz., Haplostyla, Dispathostyla, Tetraspathostyla, and Heterospathostyla.

The HAPLOSTYLA (ἁπλους, simple; στυλος, pillar) embrace those species which possess a round and simply subulate dart, without any strengthening accessory blades or buttresses or any distinct apical developments or definite basal rod-like ornamentation or enlargement; these simply formed or primitive darts are often paired, the stylophores or dart-sacs occupying corresponding positions at opposite sides of the vagina.

FIG. 676.—Gypsobelum or love-dart of *Helix pulchella* Müll., ×20, showing the primitive simplicity of the weapon, and illustrating the Haplostyla.

The DISPATHOSTYLA (δύο, two; σπάθη, a blade; στυλος, a pillar) possess darts of the simply subulate Haplostylous type, with the addition of a pair of strengthening blades or buttresses placed at opposite sides of the weapon; these blades may be restricted to the free end which therefore becomes more or less enlarged, and forming in its extreme development a flattened lanceolate head, as seen in *Helix lapicida*.

In its more primitive form it illustrates the origination of a pair of lateral blades or buttresses near the apex; these, however, often do not acquire great prominence, but sometimes extend the length of the dart; the most rudimentary form of the dart is exhibited by *Helix caperata*, but *Helix virgata* shows the lateral apical blades as distinct formations.

FIG. 677. FIG. 678.

FIG. 677.—Gypsobelum or love-dart of *Helix virgata* Da Costa, × 8, with section showing the paired lateral blades, and illustrating the Dispathostyla.

FIG. 678.—Gypsobelum or love-dart of *Helix lapicida* L., × 8, with section of head, showing the exaggerated development of the paired lateral blades and their assumption of the lanceolate form.

The TETRASPATHOSTYLA (τετρας, four; σπἄθη, a blade; στυλος, a pillar) or four-bladed darts, show a great advance in complexity upon the dispathous form, chiefly by the formation of two other blades at right angles to those already present; the four blades are not always equally salient, as the pair representing the blades of the Dispathostyles may be fully formed before the more recently acquired pair are beyond the rudimentary stage, the base is usually encircled by a series of regularly arranged rodlets, encircling the basal tubercle, and the spaces between the blades may in certain species become connected together by a number of regularly disposed crescentic films. A tendency to the character of the Heterospathostyla is shown by the channeling of the outer margin of the blades, and thus forming a link with them.

FIG. 679. — Gypsobelum or love-dart of *Helix pomatia* L., × 6, with an oblique section showing the quadruple blades characteristic of the Tetraspathostyla.

The HETEROSPATHOSTYLA (ἕτερος, different; σπἄθη, a blade; στυλος, pillar) or variously edged dart-bearers, show the highest specialization attained by the dart, the four-bladed weapon of the Tetraspathes losing their simple edges, each blade splitting longitudinally and being reflected outwardly, forming double flanges to each blade, or eight edges to each dart, but occasionally towards the free end the four primary blades may project beyond the point of reflection of the flanges, each blade thus showing three edges, so that a dart with eight edges near the base will exhibit twelve towards its apex.

FIG. 680. — Gypsobelum or love-dart of *Helix hortensis* Müll., × 8, with oblique section showing the complex structure of the blades distinctive of the Heterospathostyla.

These reflected flanges are the last parts formed, as is shown by the fact that an otherwise perfect dart may occasionally be found in which the reflected parts are still quite membranous.

The STYLOPHORE (στυλος, a rod; φερω, to bear) or dart sac is an appendage to the female genital system, which secretes, protects, and protrudes the dart. It is usually a short claviform pouch opening

into the vagina below the aperture of the digitate glands, and is composed of a thick outer layer of transverse and longitudinal muscle fibres, which are thinnest at the summit of the sac, and facili-

FIG. 681. FIG. 682. FIG. 683. FIG. 684.

Dart sacs of different species of Helices, with the vaginal digitate glands, showing the evolution from the multiple to the simpler single sac.

FIG. 681.—Bifid laterally paired sacs of *Helix rufescens* Penn., × 3.
FIG. 682.—Bilaterally paired sacs of *Helix itala* L., × 3.
FIG. 683.—Unilaterally paired sacs of *Helix fusca* Mont., × 3.
FIG. 684.—Dart sac or stylophore of *Helix pomatia* L.

tate its eversion; the more delicate and glandular inner layer is adherent to the outer envelope, it is often deeply pigmented and secretes a viscous lubricating fluid.

For convenience the dart sac of the British species may be separated into two groups, in which the teliferous sacs are single or paired; both, however, may be more or less completely divided, giving an external appearance of double and quadruple sacs, but only the outer sacs develop darts, the subsidiary additional sacs which always lie nearest the vaginal passage showing no indication of ever having done so, and it is not improbable that these auxiliary sacs may be a modified form of the coronal glands present in *Zonitoides*.

In *Zonitoides* the lubricant glands are concentrated in the form of an oval pouch protruding externally near the apex of the dart sac and opening therein; this peculiar glandular outgrowth represents a remarkable feature strikingly developed in the exotic genus *Ariophanta*, in which it takes the form of a circlet of similar outgrowths around the subterminal portion of the sac; such apical glandular developments have been distinguished by Pilsbry as coronal glands.

FIG. 685.—Reproductive organs of *Zonitoides excavata* (Bean), × 10, showing the glandular outgrowth or coronal gland of the dart-sac (after photo. by W. Moss).

st. stylophore or dart sac, showing natural position of dart and character and position of the coronal gland, *c.gl.*; *p.s.* penis sheath with calcareous channeled plates; *vag.* vagina; *sp.* bifid spermatheca duct.

The SPERMATHECA (*σπερμα*, seed; *θεγα*, a sheath) is a stalked vesicle, developed in the Euthyneures and some of the Streptoneures as an addition to the female organs to receive the Spermatophore or seminal fluid from the male organs of its partner.

Usually it takes the form of a vaginal or vestibular diverticulum, with a terminal sac-like enlargement; in *Pupa*, *Clausilia*, and certain groups of Helices the stem develops an auxiliary diverticulum, known as the copulatory branch (see fig. 323, page 160), which, when well developed, far exceeds the length of the primary duct, and sometimes acquires a sac-like termination.

A most remarkable variation from the typical spermatheca, shared by the North American Gastrodontæ, is found in *Zonitoides*, in which the stem becomes divided or cleft, the chief or most capacious duct opening into the penis sheath and the other in the normal position upon the vagina; a similar feature is said to be exhibited by *Clausilia* and *Balea* and appears to culminate in the African *Trochomorpha*, in which Pfeffer could find no external opening for the male organ, the cleft spermatheca duct being therefore assumed to be a contrivance to ensure self fertilization.

FIG. 686. — Reproductive organs of *Zonitoides excavata* (Bean), × 3, showing the bifid spermatheca duct.

ot. ovotestis; *h.d.* hermaphrodite duct; *a.g.* albumen gland; *s.d.* sperm duct; *p.s.* penis sheath; *ov.* oviduct; *v.* vagina, with vaginal gland; *sp.* spermatheca with divided duct; *st.* stylophore or dart sac.

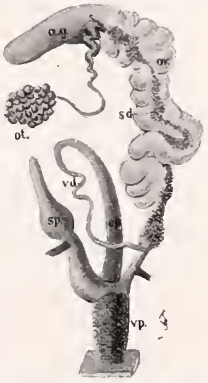


FIG. 687. — Reproductive organs of *Arion circumscriptus* Johnst., × 2, showing the vestibular gland.

ot. ovotestis; *a.g.* albumen gland; *s.d.* sperm duct; *v.d.* vas deferens; *ep.* epiphallus; *ov.* oviduct; *sp.* spermatheca, with its retractor; *v.p.* vestibular gland.

The ATRIUM (*atrium*, an entrance-hall) or Vestibule, is the thick-walled and often longitudinally ridged spacious cavity opening to the exterior and within which the various organs of the reproductive system converge; it may also contain the Sarcobelum, or excitatory organ, and is enveloped exteriorly in *Arion* by a compact and dense glandular pad, whose secretions are discharged directly into the vestibule.

Reproduction in the mollusca is invariably sexual and entirely dependent upon the complete activity of the generative organs, as although the ovum without fertilization undergoes segmentation up to a certain stage, yet the stimulus of the male element is essential to successful and regular development.

Some of our species are extremely prolific, as many as two million eggs being estimated by one observer as the annual production of a large *Anodonta cygnea*, and although all our species by no means approach this enormous rate of increase, yet a sufficient number generally survive to enable the different species to maintain their ground, their multiplication being effectively counteracted by numberless enemies and dangers, otherwise we should in a short time be literally overwhelmed by the vast numbers annually developed.

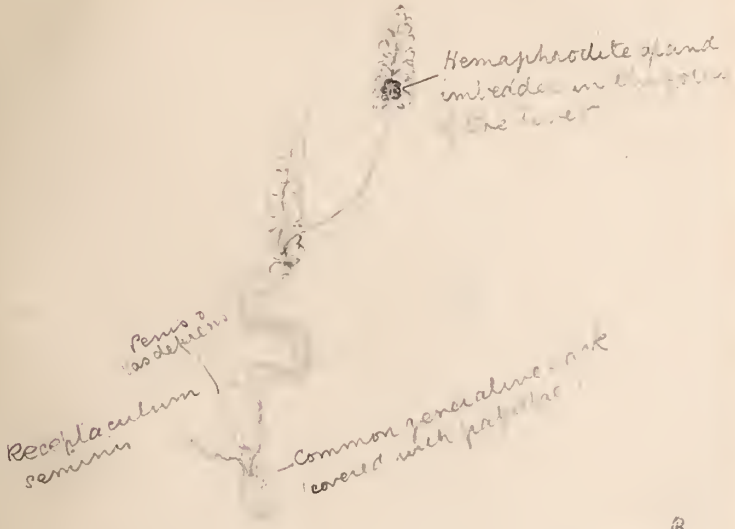
Pairing does not take place in the Pelecypoda or in the more archaic Gastropods, which are unprovided with the necessary organs for the purpose, but all phalliate species exercise this power, although in remarkably diverse ways.

Fig. 688.—Love-making or courting of a sinistral and dextral *Helix aspersa* Müll, modified from a nature sketch by W. H. Heathcote, F.L.S.

The preludes to the sexual act vary in the different species, certain of the slugs marching round and round in a slowly contracting circle and also mutually patting, caressing and fondling each other with their tentacles, labial lobes and egersidia, and devouring the mucus from each others bodies; the Arions also consume the accumulated mucus upon the caudal gland of the prospective partner, which has probably some excitatory effect upon the animals and possibly hastens the desired conjugation.

Some Helices during their preliminary manœuvres not only make use of their love darts, but mutually touch and caress with their

Arion hortensis



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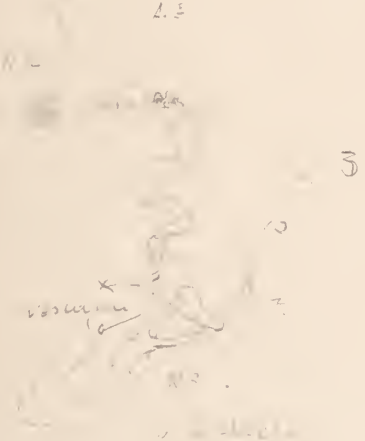
Arion hortensis. Generative organs 12/8/50

The muciparous gland does not appear

Do the papillae on the surface of the common generative sack take its place

Arion circumscriptus



tentacles, which are curiously drooping at the tips during this period, possibly from the partial withdrawal of the blood to other organs; they also frequently simultaneously elevate the anterior portion of their bodies, bringing the raised part into close, but temporary, apposition, touching and rubbing against each other and probably increasing the mutual excitement by the use of their love darts.

Fig. 689.—Pairing of *Limax maximus* L., slightly modified from a nature sketch by L. E. Adams, B.A.

In the Dicœciate species and certain of the Monœciate Ditremata, the conjugation is simple, one individual being male or acting as male only, the partner being female or fulfilling feminine duties exclusively, the necessary conjunction being effected usually after probably some preliminary coqueting.

In the Monœcia, the conjugation is generally more complex, as fertilization is reciprocal in many species, each individual simultaneously fulfilling the rôle of both male and female with another individual. The amorous caresses of the Monœcia, which precede their conjugation, are also striking and long continued, and may, in some species, be continued for the space of ten hours, certain highly specialized and remarkable organs, the Egersidia, being developed for excitatory purposes.

In *Limax maximus* and certain other species, the prospective pair after their voluptuous preludes and circular promenade, suspend themselves heads downward from some suitable spot by a conjoined strand of mucus mutually intertwining their bodies and the essential organs being exserted and also externally intertwined in a very complicated manner during the act.

Fig. 690. — Pairing of *Limnæa peregra* (Müll.).

In the Ditremate *Limnæa* although the effect of the pairing of two individuals is that one only is fertilized, as in the Dicœcia, yet on account of the widely separated apertures other individuals may join the original pair and

one perform the part of male to the individual already acting as the male, while another specimen may perform the female part to the one of the original pair acting as female, which acts as male to the newcomer; even then the number of animals taking part may still be similarly added to and a chain of animals formed, of which all except the terminal individuals will be reciprocally fertilized.

Some observers have expressed the opinion that some species, as *Helix aspersa*, pair but once, as although isolated after a single pairing, they have been observed to continue to deposit fertile eggs for four successive seasons; this phenomenon may, however, arise from the retention and continued vitality of the spermatozoa or from autofecundation, but it is certain that many species may pair frequently at short intervals, as is occasionally shown to be probable by the fragments of several love-darts amongst the viscera (f. 671, p. 366), or more undeniably by the presence of two or more spermatophores within or near the spermatheca.

FIG. 691.—Rival Spermatophores within the spermatheca of *Almalia sowerbyi* (Fér.), × 6, showing the result of a second pairing; the second spermatophore finding the appropriate quarters already occupied, bursts through the walls of the sac.

Pairing has also been found to occasionally occur not only between closely allied species, as *Helix nemoralis* and *H. hortensis*, but also between species usually considered perfectly distinct or even between different genera, as between *Pupa* and *Buliminus*. The union of *Stenogyra decollata* and *Helix pisana* has been chronicled by Gassies, the resultant hybrid progeny, though often scalariform and bizarre, usually resembling their mother.

The SPERMATOZOON (σπερμα, seed; ξοον, animal) or Zoosperm, the essential male element, is a minute highly specialized motile cell, resembling an active protozoan or flagellate infusorian and is usually a filiform body with small cephalic enlargement, almost wholly composed of nuclein or chromatin, and a filiform contractile tail which may have a dilated extremity; it possesses great vitality, enduring great extremes of temperature, and may retain its fertilizing powers for lengthened periods; it is paralysed by acids and stimulated by alkaline substances.

In the hermaphrodite species the spermatozoa and ova are developed within the ovotestis; ripening more or less alternately, the spermatozoa

North Grange,

Horsforth.

oct 1904

Dear Sir/

I am glad to hear that you so cordially approve my work & that you propose aiding me as far as possible

I regret that the figure of Sowerbyi does not come upto your expectations I think you may rely on its accuracy- the mucus glands are very difficult to render satisfactorily they would perhaps have been rendered better by a wash drawing but the outline method is preferred by most

I shall be glad to see your drawings of the Arions. As far as possible I restrict myself to the work in hand & even then

I find many, very many things hinder my progress.

I have all the drawings of the alimentary canal, sexual organs jaws teeth &c of the Arions most engraved.

I am striving to get out Part X as quickly as possible.

Any of your records will be useful to me & I shall be glad of them, so shall be pleased to get your Catalogue.

Kindest regards

Jno W Taylor

North Grange,
Horsforth.

Dear Mr Reynell

I have looked carefully over your anatomical Sketches with considerable pleasure — Some parts are very beautifully done

Both the pencil Sketches seem to belong to A. circumscript: the seeming duct is probably the retractor muscle see my Sketch Vol. I p 371

If you should make a dissection drawing of Vitrina pellucida I should be glad to see it

It is so refreshing to meet with an anatomical worker in this branch who does the work carefully & conscientiously the usual drawings of dissections are very slovenly & very inexact

Kindest regards

Yours truly

are usually first developed and are arranged with their heads to the walls of the gonad in intimate connection with the nutritive cells, and are shed from the germinal epithelium in the form of mother cells or

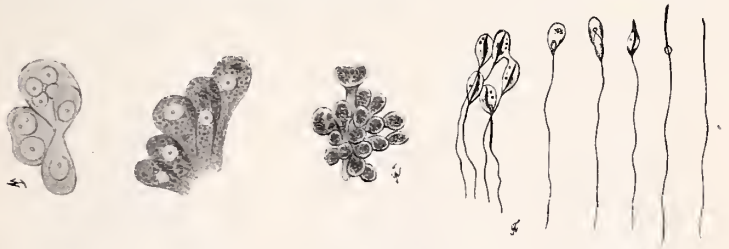


Fig. 692. Fig. 693. Fig. 694. Fig. 695. Fig. 696.

Development of the Spermatozoa of *Cyclostoma elegans* (Müll.), highly magnified (after Garnault).
Figs. 692, 693.—Groups of Spermatogonies. Fig 694.—Group of Spermatocytes.
Fig. 695.—Cluster of immature Spermatozoa. Fig. 696.—Maturing and mature Spermatozoa.

spermatocytes, which mature and separate into their constituent spermatozoa whilst free within the lumen of the lobule, the ova retaining their position upon the epithelial walls until mature.

In certain diœcious species two forms of spermatozoa may be found —an elongate one with a caudal filament and spirally twisted head, the other long, cylindrical, and slender, without any cephalic enlargement, but with a terminal tuft of extremely fine filaments; these are affirmed to be formed by an agglomeration of miniature spermatozoa and were at one time regarded as parasitic organisms, Ehrenberg applying the name of *Phacelura paludinæ* to the form peculiar to the *Paludinidæ*.

Fig. 697.—Dimorphic spermatozoa of *Vivipara vivipara* (L.), greatly magnified (after Recluz).

The spermatozoon has a vermicular or axial rotatory motion, and when in contact with the egg has been noted in some forms of life to move around the ovum in regular circles of varying orbit, so that it eventually meets the micropyle or minute aperture leading to the interior of the egg, fusing with the protoplasm projecting therefrom and losing its enveloping membrane, which fuses with the egg membrane and closes the micropyle against other spermatozoa. If polyspermy results owing to cold or weakness of the ovum it may give rise to abnormal offspring.

Fig. 698.—Fertilizing receptacle of *Succinea putris* (L.), × 20 (after Ihering), showing its connection with the seminal vesicles, etc.

v.s. seminal vesicles; *h.d.* hermaphrodite duct; *ov.* oviduct; *v.d.* vas deferens.

The Spermatophore (σπερμα, seed; φέρω, to bear) or Capreolus, is a variously shaped elongate body, composed of the hardened secretions of the walls of the flagellum, the epiphallus or the widened part of the vas deferens. It is usually a flexible but firm husk, which becomes brittle on exposure, usually closed at one end and open at the other, and containing zoosperms. The Spermatophore owes the

Fig. 699.

Fig. 700.

Fig. 701.

Fig. 699.—Spermatophore of *Helix virgata* Da Costa, × 4.

Fig. 700.—Spermatophore of *Amalia sowerbyi* (Fér.), × 6, in situ, as secreted by the epiphallus.

Fig. 701.—Spermatophore of *Amalia sowerbyi* (Fér.), × 6, in situ, after transference to spermatheca of partner.

remarkable shapes and complicated denticulations it assumes in the different species to the character of the cavity in which it is formed or moulded. Its function is to more perfectly ensure the transfer of the spermatozoa from one individual to the spermatheca of another during the process of pairing.

The Ovum (*ovum*, an egg) may be regarded as a modified epithelial cell, corresponding not with the spermatozoon but with the mother sperm-cell, the division of the nucleus of the ovum and the expulsion of the polar globules being paralleled by the repeated division undergone by the sperm cells. The ovum encloses within the vitelline membrane a clear nuclear fluid or nucleoplasm with minute nucleoli and a complex system of filiform coils or loops which contain the germ plasma of Weissmann; it is externally enveloped by an albuminous layer and surrounded by an excessively thin, shining and transparent membrane or chorion, which may acquire opacity and hardness from the gradual deposition upon its inner surface of large rhomboidal crystals of carbonate of lime, forming an exquisite microscopic object; the lime deposit may, however, be confusedly granular, while, in certain terrestrial species, the external envelope may be calcareous or, as in the *Limnæidæ* and *Succineæ*, the egg membrane may be soft and

transparent and the eggs aggregated and enclosed within a mass of albuminous matter.

The egg originates upon the walls of the lobules composing the gonad, and in its early stages resembles an amœboid cell, but becomes rounded and encysted by the reception and storage of nutritive matter, through the micropyle, an opening in or prolongation of the vitelline

FIG. 702.—Ovarian ovum of *Helix aspersa* Müll., greatly enlarged (after Huxley and Martin), showing micropyle.

FIG. 703.—Lobule of the ovotestis of *Helix hortensis* Müll., highly magnified, showing the maturation of spermatozoa within the lumen of the lobule and of ova upon its walls (after Gegenbaur).

membrane, by which the ovum is fixed to the ovarian walls during development, and through which the spermatozoon usually enters for fertilization; this aperture in ova not perfectly mature may be stopped by a peculiar lenticular body, known as Keber's corpuscle.

The eggs of the terrestrial species are usually deposited, a few days after pairing, in moist and shady places, the animals often forming an oblique excavation in the earth for the purpose, in which they partially bury themselves during the process, the tentacles being contracted, and an interval of four, five or more minutes elapsing between the deposition of each egg, the duration of the process occupying from twenty to forty hours.

After deposition the eggs increase rapidly in size, for the mass deposited may, owing to this property, in twenty-four to thirty hours exceed the total bulk of the animal.

The eggs of aquatic Gastropods are generally affixed to plants, stones or other submerged objects, and *Neritina* attaches them sometimes also to the shell itself and that so securely that a part of the egg shell may remain permanently fixed to the shell or other surface to which it may be applied.

FIG. 704.—Egg capsules of *Valvata cristata* (Müller), greatly enlarged (after Moquin-Tandon).

The ova of some species are placed in variously shaped capsules or ovisacs secreted by the walls of the oviduct, each capsule containing a number of ova, arranged in special modes, peculiar to the different species; although in *Neritina fluviatilis* only one egg in a capsule becomes developed, the rest discontinuing development at or before the

first processes of cell division, the embryo devouring the rest of the ova in the capsule, which thus supply it with nutriment.

The Ontogeny (ὄντο, being; γένος, race) or development of the individual from the ovum, known also as Embryology, during which the embryo passes through a series of larval stages or phases of development before acquiring adult form, which are a condensed and modified but evanescent repetition or recapitulation by the individual mollusk of the various forms and characters possessed by the whole chain of its ancestors, and is, therefore, an epitome of the Phylogeny or development of the race.

Upon the maturation of the egg, and before its fertilization, it separates from the ovarian wall, the clear protoplasm accumulating at the animal or formative pole, and the darker food yolk forming the opposite and larger segment distinguished as the vegetative or nutritive pole. The nucleus approaches the walls of the vitellus at the formative pole and divides mitotically, one half the nucleus being expelled as the first polar globule or directive corpuscle, the remaining moiety of the nucleus again undergoing division, and half the remaining nuclear matter is extruded as the second polar globule, thus leaving the germinal vesicle with only one-fourth of the nuclear matter originally present, which is then known as the female pronucleus.

Fig. 705.—Egg of *Limnæa stagnalis* (L.), showing its first segmentation and the expulsion of the polar globules, highly magnified (after Ray Lankester).

Upon fertilization the head of the spermatozoon fuses longitudinally with the female pronucleus, and transverse segmentation or cell division of the combined nucleus takes place at the limit of its growth, the direction of the cleavage furrows being equatorial or meridional, according as they coincide with or are perpendicular to the chief axis.

Fig. 706.—Early embryo of *Pisidium pusillum* (Gmelin), highly magnified, showing the meridional and equatorial cleavage grooves (after Ray Lankester).

The segmentation of the nucleus may be direct or indirect.

Fig. 707.—Direct or Amitotic cell division, showing the nucleus in process of separating to form two daughter nuclei (after Carnoy).

Amitotis (ἀ, without; μιτος, thread) or direct division only takes place as a rough and ready means of division of the larger cells and rarely occurs.

It is accomplished by the elongation of the nucleus, which becomes dumb-bell shaped; the neck becoming further constricted and eventually dividing, forming two cells, the whole process being very rapidly accomplished.

Mitosis (*μιτος*, thread) or indirect segmentation is the prevalent mode of nuclear division and ensures a more perfect dividing of its chromatin elements; the process is characterized by the enlargement of the nucleus and the appearance of beautiful spiral stars. It is always preceded by the resting condition, the chromatin or stainable part having then the aspect of a complexly coiled thread, which gradually becomes more distinct, and breaks up into a number of sections or loops, the nuclear membrane and nucleoli disappearing, and the centrosomes becoming apparent at opposite poles; these constitute the foci of a characteristic arrangement of protoplasmic fibres forming the spindle figure, the chromatic loops become arranged around it at the equatorial plane and contribute to form the Monaster or

Fig. 708. Fig. 709. Fig. 710. Fig. 711. Fig. 712. Fig. 713.

Diagrammatic figures representing various stages in the Mitotic or indirect segmentation of the nucleus (modified after Waldeyer).

Fig. 708.—Resting nucleus, showing the encircling nuclear membrane, nucleolus and chromatin network.

Fig. 709.—Polar view of "Loose Skein" stage, with centrally and excentrically disposed loops.

Fig. 710.—Monaster stage, as seen from pole. *c.* cytaster or polar star; *ch.* cleft chromosomes, radially disposed.

Fig. 711.—Monaster stage, viewed laterally. *c.* cytaster; *ch.* cleft chromosomes radially arranged around *s.*, spindle figure.

Fig. 712.—Dyaster or Twin-star stage, viewed laterally. *c.* cytaster, *ch.* cleft chromosomes separated and travelling along the spindle figure towards the poles to form the daughter nuclei.

Fig. 713.—Separated nuclei, but cell protoplasm not yet divided. *s.* remains of spindle figure in hilus of chromatic figure; *h.* hilus or pole; *d.* line of impending separation of the protoplasm of the two cells.

equatorial plate, the angles of the loops being towards the centre of the spindle figure and the limbs projecting peripherally; the loops afterwards split longitudinally, the divided halves separating and travelling along the spindle threads to opposite poles to form twin daughter stars and constituting the Dyaster stage. These processes are accompanied by a constriction of the cell, transversely to the axis of the spindle, which continues until it is divided into two separate cells, the spindle, centrosomes, etc., disappear, and the chromatin of the now separate nuclei each acquire a new nuclear membrane and assume the resting condition prior to a repetition of the process.

The eggs of our British species contain comparatively little stored-up food-yolk and the segmentation is therefore complete or Holoblastic (ὅλος, whole; βλαστη, bud) and only exceptionally incomplete or Meroblastic (μερος, part; βλαστη, bud) as in the Cephalopoda, in which a large part of the egg is formed of nutritive substances and takes no part in the division, which is always most active and complete at the animal or formative pole.

The segmentation cellules, however, vary in size and are distinguished as Micromeres and Macromeres, the cleavage process being known as Equal Segmentation when the cellules are approximately equal in size, and Unequal Segmentation when they are markedly different.

The Micromeres or segmentation cellules of the animal pole are small and poor in nutritive yolk, they originate at the point of expulsion of the polar bodies, and give rise to the ectoderm, the mantle, the embryonal and adult organs of locomotion, the nervous and sensorial systems.

Fig. 714.—Egg of *Bithynia* at formative pole, showing the unequal segmentation of the vitellus into macromeres and micromeres (after Pelseneer).

The Macromeres, or nutritive cellules, are larger than the Micromeres, and richer in yolk, they divide more slowly and occupy the opposite pole, and constitute the Endoderm, retaining the primitive functions of receiving and digesting food.

The Morula (dim. of *morum*, a mulberry), Polyblast or Blastula, constitutes the first stage of development, the segmentation having been continued until the vitellus has externally the aspect of a uniform mulberry-like mass of nucleate cells, the interior forming the segmentation cavity or Blastocœl.

Fig. 715.—Morula stage of *Pisidium pusillum* (Gmelin), highly magnified (after Ray Lankester).

The Gastrula (dim. of γαστὴρ, the stomach) forms the second phase of development, and has the form of a sac, its ectoderm or outer layer being formed by the micromeres, and the inner layer by the macromeres or endoderm cells, the gastrula arising in those eggs with little food yolk by the emboly or invagination of the macromeres or vegetative cells within the more rapidly multiplying micromeres or formative cells, but where more food-yolk is present the gastrula is formed by epiboly or overgrowth of the macromeres by the micromeres, as in *Sphærium*, etc.; the invagination is known as the

Archenteron, or primitive digestive cavity, and its opening at the nutritive pole is the Blastopore (*βλαστὸς*, a bud; *πόρος*, a passage) or elongated primitive mouth of the Gastrula; it usually becomes gradually closed, the middle part forming the foot, an invagination in its anterior part constituting the stomodæum or œsophagus, and the proctodæum or anus arising in its posterior part, both communicating with the Archenteron or digestive cavity.

FIG. 716.—Median section of Gastrula stage of *Viviparа*, seen from left side, greatly enlarged (after Erlanger).

bl. blastopore; *bl.g.* blastoporic groove; *a.* archenteron or primitive digestive cavity; *b.* blastocœl or segmentation cavity; *ec.* ectoderm; *en.* endoderm; *m.* mesoderm; *c.* cœlom; *v.* velum.

The ectodermic outer envelope of the gastrula, and its invaginated endoderm, enclose between them a cavity, the blastocœl, which eventually becomes the blood space or Hæmocœl (*αἷμα*, blood; *κοῖλος*, cavity), and acquires chiefly from the endoderm a cellular tissue, the Mesoderm (*μέσος*, middle; *δερμα*, skin), which becomes split up into numerous sinuses and separates into a somatic or exterior and a splanchnic or internal layer, originating the reproductive and excretory organs, the muscular system, the heart, and circulatory system generally.

Contractile sinuses arise in the cephalic region and in the walls of the body, a large posterior sinus or caudal vesicle may also be developed, which contracts alternately with the somatic or cephalic vesicles, and temporarily serves to circulate the fluid through the body before the developing heart becomes functional.

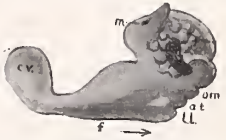


FIG. 717. — Embryo of *Agriolimax agrestis* (L.), greatly enlarged (after Van Beneden and Windischmann) showing the well developed pulsatory caudal vesicle.

l.l. labial lobes; *c.v* caudal vesicle; *m.* mantle; *om.* ommatophores; *f.* foot; *a.t.* anterior tentacles.

The arrow indicates the direction of the rotation of the embryo within the egg.

The TROCHOSPHERE (*τροχός*, a hoop; *σφαιρα*, ball) stage still retains a bilateral symmetry of the organs, the torsion of the body and the approximation of the two ends of the alimentary canal not having yet been accomplished. It is remarkable for the barrel shape of the embryo and the possession of a cilial investment which is most distinctly developed as a preoral girdle or ridge, which forms a characteristic feature of

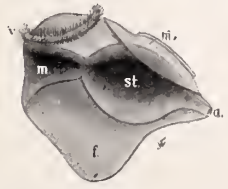


FIG. 718.—Trochosphere of *Viviparа* (enlarged after Bütschli).

m. mouth; *v.* velum; *st.* stomach; *a.* anus; *f.* foot; *m.* mantle and shell.

the Trochosphere stage; their action sets the albuminous contents of the egg in motion, and facilitates the inception through the egg membrane not only of oxygen, but of the nutritive matter from the enveloping albuminous mass within which some eggs are enveloped; it also establishes a kind of vortex in which the embryo itself is gradually involved, so that it begins an oblique rotatory movement upon its own axis, with the anterior part of the animal in front, varying in rapidity according to temperature and age, and eventually also revolving around the internal walls of the egg cavity; this complex motion has been happily likened in a general sense to that of the diurnal and annual rotation of the planetary bodies around the sun, and continues up to the time the embryo can perform voluntary movements.

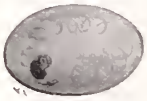


FIG. 719.—Early embryo of *Limnæa peregra* (Müll.), highly magnified (modified after Dumortier), showing the general character of the embryonal rotation.

The arrow indicates the direction of the motion.

The VELIGER (*velum*, a sail; *gero*, I bear) stage is distinguished from the Trochosphere by the more distinct development of molluscan attributes, by the torsion of the visceral sac, characteristic of adult Gastropods, and especially by the enlargement of the anterior region, to form the Velum, which may be prolonged into lobes or processes fringed with powerful cilia, and constitute the organs of locomotion persisting in the adult of *Limnæa* as the subtentacular lobes.

In the terrestrial and fluviatile genera the animal hatches out in the adult form, the various larval stages being very transient or even suppressed and passed through within the egg. The Velum is not therefore needed as a locomotory organ and is reduced to one or more rings of cilia, but in most marine species and in *Dreissensia* the embryo is hatched early as a free swimming Veligerous larva, the highly contractile and well-developed pre-oral ciliated velar lobes not only acting as organs of locomotion, but probably also assisting in respiration and circulation.

FIG. 720.—Veliger stage of *Dreissensia polymorpha* (Pallas), with velum extended, greatly enlarged (after Korschelt).

v. velum fully extended and showing pigmented median area; *sh.* shell; *p.* pigmentation beneath oral aperture.

Certain groups, probably owing to special dangers to their offspring, have acquired the habit of retaining the ova within the body until the hatching has actually taken place, as in *Vivipara*, *Anodonta*, and certain species of *Pupa*, *Clausilia*, *Helix*, etc., the young being

nourished by the secretions of the brood pouch, within which they may remain, as in the *Sphæriidæ*, until they are fully one-third the size of the parent shell.

In the *Unionidæ*, although the earlier phases of their development are passed through within the gill-cavities of the parent, the larvæ upon exclusion adopt a parasitic life, fixing themselves upon the fins or gills of fishes and becoming encysted thereon by a pathological development of the tissues of the host, but are so different from the adult animal that they were formerly described as independent parasitic organisms under the name of *Glochidium parasiticum*, and it is only after a secondary metamorphosis, undergone during encystment, that they assume the adult form.

FIG. 721.—Embryos of *Unio*, encysted upon the gills of a Perch, greatly enlarged (after Pelseneer).

Experiments have demonstrated the power of mollusks to reproduce or renew the mantle, the foot, the tentacles, or even the head when these have become injured or separated by accident or design, but it is essential that the cerebral ganglia should not have sustained serious injury. Certain extra-British species are known to spontaneously and voluntarily cast off the hinder part of the foot when in danger, taking advantage of the circumstance to escape.

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The GEOGRAPHICAL DISTRIBUTION of the terrestrial mollusca over the surface of the earth is a subject fraught with many abstruse but interesting problems, bearing not only upon the origin of the various species and groups but upon that of the entire animal and vegetable kingdom.

Although the more simply organized and primitive forms are now so widely diffused, it is owing chiefly to their vast antiquity that this has been accomplished, as the dispersal of the terrestrial species is but slow, and almost invariably across more or less intimately connected tracts of country, their range in time enabling them to take advantage of the probably numerous geographical changes and varied land connections to overspread the globe.

The simpler and more primitive the species or group and the more ancient its origin, the wider but more discontinuous is its range in space, while the more complex and recent forms have a comparatively restricted yet more compact distribution.

Distribution or dispersal has, however, doubtless been influenced by the climatal changes the globe has undergone, these fluctuations having been such that at no distant date a colder climate extended over a large part of the northern hemisphere, and although the severity of this epoch would appear to have been greatly exaggerated, yet it was undoubtedly accompanied by the formation of extensive glaciers. These frigid conditions were preceded by a warmer miocene period, during which deciduous trees and evergreens flourished within ten degrees of the pole, but these changes of climate were so excessively slow, that if any power of adaptability be conceded to organized life, we are compelled to allow that most of the less severe changes would have been guarded against by suitable modifications of the organisms in response to the gradually changing conditions to which they were subjected.

The changes of habitat by most species are, however, not due merely to climate, but to the evolution of more advanced races, whose migrations are the chief cause of the restriction of the less adaptable and more ancient forms of life to remote, inclement or isolated regions, where they are temporarily comparatively free from the competition of more advanced forms; arctic animals and plants are not following the colder conditions from preference, but because they are compelled by the stronger forms to fall back and adapt themselves to cold or barren stations not occupied by the stronger races.

The physical obstacles to uniform dispersal are mountain chains, deserts, marshes, rivers, arms of the sea, or any natural features dissimilar to those to which the particular species is more especially adapted. Some of these barriers to dispersion have apparently been permanent through vast geological periods, but in other cases effective barriers have been formed after considerable diffusion of the earlier types of life has taken place.

Islands, especially in the warm and tropical zones, are often exceedingly rich in mollusca, and sometimes exhibit faunæ which are remarkably distinct, owing to the survival and external modification therein of archaic forms of life which were formerly much more uniformly dispersed over the globe, but which have long ago been exterminated or driven off from the neighbouring continental lands in which competition is more active; the British Isles, however, do not possess a special and peculiar fauna, their isolation being too recent to show any but the slightest differentiation from the continental forms.

The classical researches of Pilsbry, Semper and others into the organization of the Helicidæ, in connection with information derived from other sources, enable us to indicate the probably true place of origin of the chief types of structure, not only of Helicidæ but of other more important groups, and to sketch out a probable route by which the earth has become populated, for although evolution in a lesser degree is a characteristic of every region, the theatre of the evolution of the great groups of all forms of life appears to have been much more restricted, and a consideration of the circumstances inclines one to the belief in a chief evolutionary area, in which have arisen the more important types of structure at present inhabiting the globe.

The Place of Origin of the chief types of terrestrial organized life is the Eurasian tract, which is the largest land mass upon the globe, embraing all the cool and temperate parts of the old world and having but few absolutely insuperable barriers, there is a freedom of communication with a consequent rivalry and struggle for existence and supremacy of such intensity that those forms of life able to maintain themselves upon this extensive continental region exhibit a superiority of adaptability and organization with an ability to prosper and increase under adverse conditions, which enables them easily to overcome the more archaic species inhabiting restricted or insular areas with which they come in competition and also to dominate the life of all other parts of the globe.

The organisms of Europe, especially of North Central Europe, being the most advanced in development, show this superiority in the most marked degree, and as may be expected from their stronger yet more adaptable character and consequent greater power of successful dispersal there are few peculiar species, and these consist chiefly of archaic and weaker types, which have not yet been eliminated, but are being gradually isolated or otherwise driven to the confines of the region before becoming finally extinct.

This pre-eminence of its organic life may be partially consequent upon the diversity of its surface and the genial, yet bracing, climate it enjoys, free from the great extremes of heat and cold characterizing Siberia, Central Asia and even Eastern Europe, characters due to its permeation by the sea, and to the prevalence of genial westerly winds bringing moisture and warmth from an ocean whose temperature is modified by the gulf stream.

The invigorating climate and variety of terrestrial conditions, combined with the complex nature of the organic environment, tends to confer a marked degree of adaptability on the species living therein, while the greater bionomic uniformity characterizing other divisions of the globe leads to a more exact adaptation with the special environment and favours high specialization, with consequent decrease or loss of adaptability to conditions other than those with which their variation is correlated, so that without prejudging the position of the chief centre of active evolution during former arrangements of land and water, we are led by these and other considerations and under present conditions to regard the North Central European region as the birth-place of the chief types of life at present occupying the terrestrial portions of the globe; and, as progress is dependent not merely upon the nature of the physical but more essentially upon that of the organic environment, it is only by association with and competition amongst the strongest and most advanced races that the highest excellence or development can arise, so that we must still look to the North Central European region for the continued evolution of the most adaptable and dominating forms of life, which the excessive severity of the life struggle will inevitably evolve.

As although tropical climes conduce to the development of species of large size, brilliant colouration and a wondrous variety of ornamentation, yet, probably partially owing to the weakness of their organic environment, they chiefly differentiate externally or specifically, by

external adaptation to modified habits or environment without the marked structural advance that would probably ensue were the associated and competitive organisms themselves more highly developed; this is demonstrated by the fact that in Australia and other remote regions of the globe occupied by the lowlier forms of life and which have not yet been invaded by the most advanced races, although a rich variety of species are developed, there has been little or no material advance in structure.

The place of origin of the mollusca and other terrestrial organisms has, however, by most writers been located in the remote, inaccessible and comparatively unknown regions of Central Asia, a belief based mainly upon a mathematical calculation fixing a central point in the range of species, the presence there of a maximum number of species of certain genera belonging to more generalized forms of life than those of Europe, the discovery of more numerous fossil remains or in earlier strata than the beds of Europe containing similar relics and the absence of any evidence that the forms now confined to Asia have ever inhabited the extreme North or South of Europe.

Unless, however, a group be a dominant one, its original home is not necessarily indicated by the aggregation at the present day of its constituent species, as the true evolutionary area of a group when no longer dominant may not retain even a single representative of the genus or family, its species having been expelled or overcome by the stronger forms which have arisen and supplanted them, while the geological record is confessedly too incomplete and fragmentary to overthrow conclusions based upon the solid facts of structure and geographical distribution by the merely negative evidence it may offer, evidence also peculiarly liable to continual correction and alteration by the results of future research and discovery; therefore, so far from agreeing with the theory of the eastern origin of the various forms of life or the reasoning by which it is supported, I regard the Central Asiatic plateau and Asia generally in a lesser degree as an asylum where those weaker or less adaptable forms of life still exist, which have migrated or been expelled from the regions more immediately adjacent to the active evolutionary centre by the intense pressure and competition of the highly organised and more adaptable forms, which will inevitably in process of time invade their present refuge, only in turn to be dispossessed by the still more advanced forms which will assuredly follow.

These improved races as evolved become the dominant ones and rapidly increase in numbers, so that dispersal becomes a necessity, and they will therefore gradually spread and drive before them to the mountains, the deserts, or to more remote or inhospitable districts those of the preceding occupants with which they enter into the closest competition, and this, not necessarily by means of active

FIG. 722.—Map illustrating the geographical continuity of distribution and the occupation of the primary evolutionary area by the dominant Pentatæniate Helicidæ (*Helix pomatia*, etc.).

FIG. 723.—Map broadly illustrative of the distribution of the less advanced yet comparatively highly organized genera *Helicella* (of which *Helix virgata* may be considered as a type), *Helicodonta* (which embraces *Helix obvoluta*) and *Helicigona* (of which *Helix arbustorum* is representative), and shewing the progress of their expulsion from the primary evolutionary area and the initiation of discontinuity of distribution.

conflict or perceptible struggle, but because the invading organisms are more adaptable to the climatal or other vicissitudes of the environment and will under comparatively unfavourable conditions prosper and increase in numbers. The range of a dominant species is thus geographically continuous, while that of a dispossessed or weaker species becomes disconnected or discontinuous, owing to their isolation in various more or less undesirable districts, where, however, for a period they will be dominant species, dispossessing in turn the relatively still weaker previous occupants, and becoming specialized by adaptation to the more extreme conditions to which they are subjected and probably thus obliterating hereditary ancestral features and originating new racial or specific characteristics.

The DIFFUSION of an improved race, or one filling some previously inadequately occupied sphere, whether of man or of more lowly organisms, from this assumed centre of dispersion, is governed by the same great laws and principles, the occupation by the stronger races of the more desirable regions adjacent to those already inhabited, and the eventual more or less complete expulsion therefrom of the more primitive and competitive species, the dispersal varying in rapidity and direction not only according to the vigour of the species already occupying the region, which may more or less successfully retard effective dispersal in certain directions, but also by the nature of the physical obstacles to be overcome; these may consist merely of districts undesirable to occupy, or may be desert lands, arms of the sea, broad expanses of water, rivers, or mountain ranges, all of which interpose obstacles to dispersal which can only be overcome by ages of time, the more feeble species being eventually compelled by the pressure of the improved races to adopt new habits of life less actively competitive or adapt themselves to the more inhospitable districts, characterized by extremes of physical or climatal condition to which they are driven, or be gradually exterminated, and we thus in temperate climes acquire a mountain, desert, or other fauna, which is representative of forms of life which may be allied to but is of earlier and more generalized type than those occupying the more desirable regions of the plains.

The VERTICAL or Hypsometrical and Bathymetrical distribution of the mollusca and other organisms is subject to the same general laws as those already described as governing horizontal dispersal. The phenomena have been locally studied by many authors and zones

defined, distinguished by the association of certain mollusks, with a preponderance of particular trees and other vegetation. The weakest terrestrial forms, are, however, always restricted to the more extreme localities, while the more advanced species occupy the more desirable areas of lesser altitude; the stronger aquatic species similarly inhabit the shallower waters, driving the weaker species or individuals into those of greater depth.

Periodicity, or cycles of abnormal abundance or rarity in the life of a species or group, also influences the increase and diffusion of all organisms. A group, species or variety may more or less rapidly attain a maximum of abundance and therefore dispersive power from no apparent assignable cause, though probably owing to circumstances being exceptionally favourable to the mode of life or constitution of the particular species affected; this period of abnormal abundance and consequent enforced dispersion may continue for a variable period, but sooner or later a decline sets in and the species, if not a dominant one, is gradually reduced in numbers until it may ultimately become quite rare or even extinct.

This phenomenon in a local and restricted way is known to most field-naturalists; a pond near Birmingham formerly swarmed with *Velletia lacustris* var. *compressa*, but this abnormal abundance after a time began to wane, until the species became quite rare or had arrived at its minimum in that place. *Amphipeplea glutinosa* has been especially noticed to be affected by this periodicity, and it may well be that *Dreissensia polymorpha* owes its rapid diffusion in Europe to the advent of a great maximum period of abundance, paralleled in an evanescent way by the irruptions of the immense flocks of Pallas's sand grouse into Europe, or the migrations of the hordes of Lemmings, and if so we shall doubtless observe in due course in our *Dreissensia* a diminution of its excessive numbers as its period of prosperity wanes, as the invasions or irruptions of a weaker species within a region occupied by a stronger race, filling approximately the same sphere of life, can only be of a temporary character, as the stronger species will eventually reassert its superiority and dispossess the feebler form, which will more or less quickly disappear. Possibly the fossil remains of *Dreissensia* in Europe may point to a former period of prosperity and extended diffusion, or may be merely indications of its continuous existence in the European region within which it probably originally emanated.

The Routes by which dispersal has probably been chiefly accomplished from the assumed evolutionary centre in North Central Europe, in which the highest forms of life are found and to which area the British Isles are immediately adjacent, is shown by the accompanying map, which indicates that the chief route for the occupation of Asia and America was by the narrow and comparatively fertile region lying to the north of the Central Asian desert and mountain plateau; on reaching the Pacific shores a furcation has taken place, one branch crossing by an Aleutian bridge to North America and spreading southward to the west of the great mountain chain, and eventually occupying the entire continent, while the second contingent travelled southwards, occupying China and passing into the Malayan Archipelago and Australasia or to the west towards India.

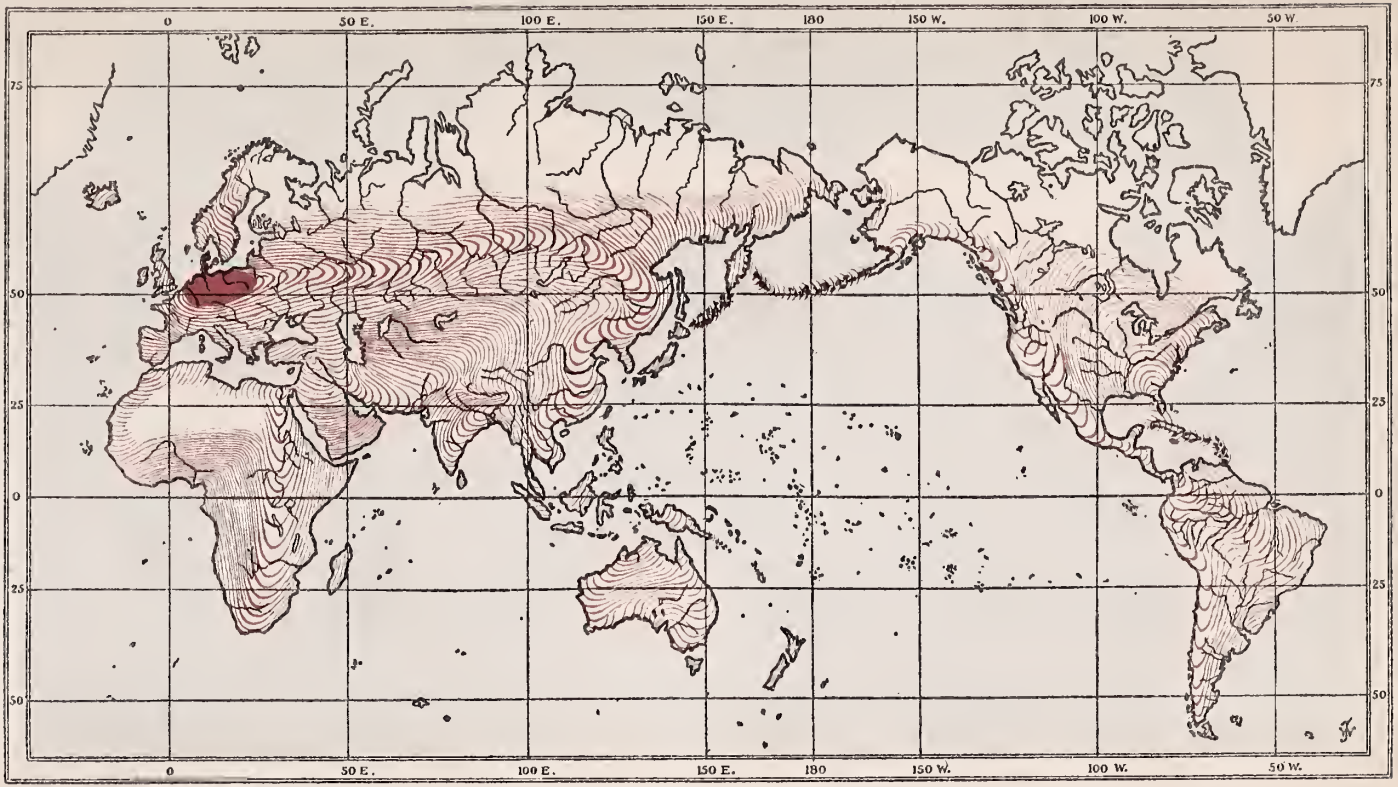
An important stream of colonists has also left North Central Europe, occupying France and the British Isles and passing across or around the mountain chains limiting the North Central European region to the south, and have occupied the Iberian, Italian and Balkan peninsulas and Asia Minor, crossing by the ancient land bridges to Africa and eventually finding their way by the Nile valley to the south of the vast Saharan barrier and opening up to the immigrants the entire African continent, while the Caucasian migrants more especially press towards the east by way of Persia and Afghanistan, more slowly overrunning the arid and elevated country to the north of Persia and to the east of the Caspian Sea.

The inclement northern region, the more inhospitable parts of the great Central Asian plateau and other similar districts become more slowly overrun by the comparatively weaker races, forced aside by the tide of stronger immigrants, and in these more inhospitable districts the relatively weaker races compelled in turn to be their occupants are successively dominant and by adaptation or specialization become more suited to the harder conditions of life to which they are exposed or become extinct.

That the routes described probably broadly represent the paths traversed in turn by the various improved races, as they became developed within the limits of the chief evolutionary area, is strikingly indicated by the distribution of the Helicidæ, whose characteristic assemblages serially representing the different stages of progress towards the most perfected type of Helicidian organization, are distributed over the globe in strict accordance with the relative perfection or

APPROXIMATE ROUTES TRAVERSED BY THE HELICIDÆ AND OTHER ORGANISMS

FROM THE PROBABLE EVOLUTIONARY CENTRE, WHICH HAVE LED TO THE UNIVERSAL DISPERSAL OF LIFE OVER THE GLOBE.



The stronger waves represent the main courses of the migratory stream; the closer rippling indicates the relative slowness of the advance.

PLATE III.

simplicity of their various parts and contiguity to the evolutionary area, the most simply organized being the furthest removed from the evolutionary centre and leaving fewest traces of their former presence therein, while in accord with increasing complexity and closer affinity to the dominant race are the occupied districts more and more closely adjacent thereto.

Although the general direction of this migration of species is undeniable, yet the most closely allied forms, from the similarity of their foods and modes of life, being naturally the most keenly competitive, tend to disperse in diverse directions, where less severe opposition than that of their closest allies is encountered, and we have in this also the explanation of the different local areas often occupied by closely related forms and the eventual restriction of their general range; thus *Helix hortensis* tends to be more northern than *Helix nemoralis*, and *Helix aspersa* more western than *Helix pomatia*, and although these species are undoubtedly sometimes found associated, this association is not a permanent one, as the weaker species must in the end eventually succumb.

There has been little mutual interchange of faunas, as has been so often affirmed, the observed intermingling being essentially due to the invasion of weaker areas by the stronger forms of life, and not to the occupation by the weaker of districts already tenanted by vigorous species, although a few primitive forms, owing to their small size, the adoption of special foods, or modes of life less actively competitive with the dominant races, may obtain or have retained a footing in districts from which most of their congeners have long been expelled.

M. Bourguignat's affirmation that mollusks can only be successfully acclimatized from North to South or from East to West had doubtless reference to his own observations in France, and in this case exactly expresses the direction in which the introduced mollusk would be placed amongst weaker races, and thus have more likelihood of prospering, at least so far as competition with indigenous forms was concerned; this principle is clearly demonstrated by the rapid diffusion of a relatively strong species when placed amongst a much weaker fauna, as evidenced by the sparrow and other forms of life in North America, the rabbit, etc., in Australia and New Zealand, the successful establishment of *Helix aspersa* at so many points of the globe, and by many other instances of the rapid increase of stronger races when placed in the midst of a palpably weaker fauna.

The Belogona Siphonadenia (*βέλος*, an arrow; *γονος*, seed; *σίφων*, tube; *ἀδην*, a gland) of Pilsbry, the most highly developed Helices upon the globe, are typically distinguished by a well-developed dart apparatus and digitiform vaginal mucus glands, characters which culminate in the subsidiary group Pentatænia (*πέντα*, five; *ταινία*, a fillet or band), of which our *Helix nemoralis*, *Helix aspersa*, etc., are examples.

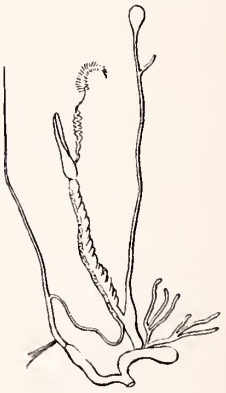


Fig. 724.—Reproductive organs representative of the Belogona Siphonadenia, *Helix* (*Tachea*) *hortensis* Müll., York.

This group is especially characteristic of the European region, where the most highly organized of the group are found, the more ancient and morphologically less perfect of the siphonadeniate forms, as *Fruticicola*, *Heliomanes*, etc., which being early evolved are more widely spread, constituting the advance guard of the new group, and have already spread over the Mediterranean sub-region and partially across Asia, intermingling with the rear of the retreating Euadeniate race, whom they have supplanted and driven off from the North Central European area, in which the Euadenia were formerly predominant.

The Belogona Euadenia (*βέλος*, an arrow; *γονος*, seed; *εὖ*, well; *ἀδην*, a gland) are a less highly organized group, possessing a simpler dart apparatus and sacculate mucus glands upon the dart sac. This group attains its greatest and most characteristic development in Eastern Asia, the genus *Helicostyla*, with its primitive dart apparatus, constituting its advanced guard in the old world, having penetrated to the tropical islands of the Indo-Malayan region; this group, however, still exists in the Mediterranean region and in Central Asia, mingling with, but retiring before, the advancing Siphonadeniate forms, the Euadeniate species being now expelled from the chief evolutionary area, except for the degenerate *Helix fruticum*, which still lingers on Central European soil, the solitary representative there of this formerly dominant race.

Fig. 725.—Reproductive organs representative of the Belogona Euadenia, *Helix* (*Epiphragmophora*) *traski* var. *cayamacensis* Hemphill (after Pilsbry).

Though this group is now a waning one in the Old World, it is the most advanced and dominant one on American soil, having crossed by the Aleutian bridge and invaded North America, but being prevented by the intervening arid and mountain regions from effective eastward extension, spreads southwards along the Pacific shores, eventually penetrating to South America and the West Indian Islands, probably reaching the latter area by way of Yucatan, as the Euadenia have not yet invaded the Lesser Antilles.

The Epiphallogona (ἐπὶ, upon; φαλλος, penis; γονος, seed), of which Pilsbry's West Indian Teleophallogona seems an earlier form, the more characteristic species of which retain an additional flagellate appendix to the male organ, is remarkable for the development of an epiphallus and flagellum upon the penis and by the total lack of the dart apparatus.

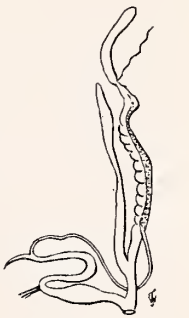


Fig. 726.—Reproductive organs representative of the Epiphallogona, *Helix* (*Planispira*) *delibrata* Benson (after Stoliczka).

This somewhat primitive group has probably originated in the same area and travelled by the path that the much later developed Euadeniate forms afterwards followed, and have been driven still further from the evolutionary centre by the Euadeniate migrants, whose advance guard overlaps the districts they occupy. Though still found in South Eastern Asia, from Japan to India, they now chiefly occupy the equatorial and tropical islands of the Indo-Malayan region and the adjacent Australian continent. They preceded the Euadeniate race in America, by whom they have been driven towards the south, occupying at the present time Central America, the whole of the West Indian Islands and Northern South America, often associated with the competitive Euadenia, but extending beyond them on all sides, except along the route by which the newer and stronger race are advancing.

The Protogona (πρῶτος, first; γονος, seed), as the still simpler forms are denominated, possess the simplest genitalia, without any accessory organs, as dart sac or mucus glands on the vagina and without epiphallus or flagellum on the penis.

This group, which formerly overspread almost the entire globe, is of still more ancient origin, and having been driven entirely from the northern hemisphere in the old world by the series of more advanced forms which successively followed them they now exist

only in the most remote regions, often separated by the ocean, mountain ranges or desert lands from species of more complex organization and greater vigour, their chief asylums being the regions furthest removed and most difficult of access from the evolutionary centre, as the extreme southern extremities of Africa, South America, Australia, Tasmania, and the more remote equatorial islands of the Indo-Malayan region, but their rear is closely pressed upon and overlapped by their epiphallophorous successors.

Fig. 727.—Reproductive organs representative of the Protogona, *Helix* (*Polygyra*) *inflecta* Say (after Pilsbry).

Eastern North America is also stocked by numerous species of this very primitive group which are there the dominant race, being shielded by the Rocky Mountain ranges from the intrusion and competition of the more highly organized Euadeniate species inhabiting the Pacific slope.

The Haplogona (ἁπλους, simple; γονος, seed) are the most lowly of the Helicidian groups and from the simplicity of their general organization are considered to stand near to the common progenitor of the Helicidæ and their close allies, and this is further emphasized by the exceedingly wide distribution their great antiquity has enabled them to attain, as representatives are found even in the Arctic regions, but throughout the Southern hemisphere the family is met with more abundantly, especially in New Zealand, Tasmania, the extreme south of South America, Southern Australia and South Africa, and is also the predominating Helicoid in the oceanic islands of Polynesia and elsewhere.

Fig. 728.—Reproductive organs representative of the Haplogona × 3, *Helix* (*Pyramidula*) *rotundata* Müll., Roundhay, Leeds.

Upon continental lands, probably from occupying different stations and their habits not directly conflicting with the dominant and higher Helicidian fauna, a few species of small size, like our *Helix rotundata*, *Helix rupestris*, etc., still exist in areas occupied by the most advanced races; but in North America we find the Haplogona represented by a number of fine species occupying the elevated and desert Rocky Mountain region, which so effectively divides the invading Enadenia from the much weaker, but predominating, fauna of the eastern states.

WORLD-DISTRIBUTION OF THE CHIEF HELICIDIAN FAMILIES,

INDICATING THE AREAS THEY NOW OCCUPY AND (IN CONNECTION WITH PLATE III.) THE CHRONOLOGICAL SUCCESSION OF THE EVOLUTION OF THEIR CHARACTERISTIC DOMINANT RACES.

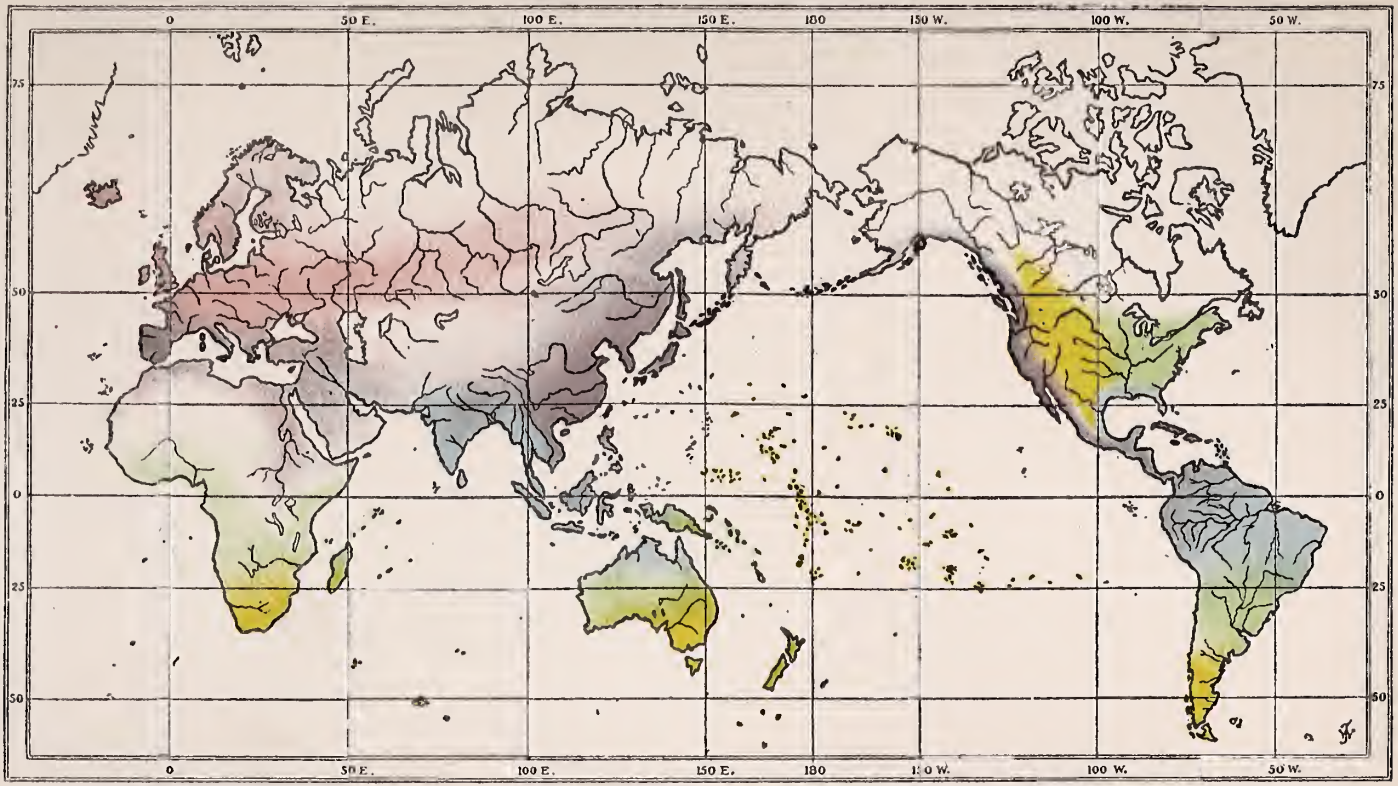


PLATE IV.

YELLOW represents the areas to which the predominance of the *Haplogona* is now restricted ; GREEN, those dominated by the *Protogona*, who are encroaching upon the haplogonous area, and are themselves being slowly over-run by the *Epiphallogona*, whose regions are coloured BLUE ; the areas of the *Belogona Euadenia* are distinguished by PURPLE, their advanced guard mingling with the rear of the *Epiphallogona*, which they are gradually driving forward, while the *Belogona Siphonadenia* (RED) in turn are invading and slowly expelling the *Euadenia* from the areas they now occupy.

The variable areas occupied by different species, which rightly understood are also an index to their relative antiquity, have led to the division of the earth's surface into a number of regions or districts to express the differences shown by one area in comparison with another. These divisions, if correct, should be broadly applicable to other forms of life and confirm the unity of the plan of development, not only emphasizing the differences in character and structure of the inhabitants, but also indicating the relative ages of the groups characterizing the divisions, and as the areas represent marked periods in migration from the evolutionary centre, the organisms inhabiting and characterizing them will change with the progress of time, and in the future, as in the past, will support groups of animals and plants different from those constituting their predominant features at the present day.

The Geographical Regions into which the globe may thus be broadly separated are known as the Arctic, Palæarctic, Nearctic, Ethiopian, Palæotropical, Neotropical, and Australasian, and these divisions, all of which may be still further sub-divided, often accord more or less closely with striking physical features either of the present day or of comparatively recent geological epochs, the more ancient and pronounced the barriers to dispersal the more striking the differences of the faunas of the districts they separate.

To illustrate the special characteristics of the different geographical regions, I have again selected as most suitable the members of the family Helicidæ, not only on account of their world-wide distribution, but because the general organization of the group has received such careful and thorough study at the hands of a number of competent observers, and their philosophical division by Pilsbry, according to the general character of their internal organization, assists us to see how beautifully their gradations of structural complexity coincide with the broad features of their distribution, so that we are often able merely from a study of the relative remoteness or contiguity of their habitat to the evolutionary area to predicate with considerable confidence the degree of structural perfection to which they have attained, as the most highly organized groups occupy the actual evolutionary area, while the most simply constituted are furthest removed therefrom, showing that the various steps leading to this greater perfection of organization have all originated within the district occupied by the latest developed and morphologically higher groups, from whence they have each in turn spread over the globe, overcoming

or driving before them their relatively weaker predecessors or isolating them within the limits of undesirable districts.

Although, therefore, the conclusions arrived at are based chiefly upon the material afforded by this important group, yet they will be found to be borne out by more extended and deeper study and will also be broadly applicable to other organisms.

The Australasian region embraces Australia, the large equatorial islands adjacent thereto, New Zealand and the islands of Polynesia, and is the most primitive zoological region, possessing only the simplest and weakest organisms, whether of mankind or other creatures. It is characterized by the presence of *Endodonta* and other of the most lowly constituted forms of life, the morphologically higher groups not yet having spread so far.

The Neotropical region, which embraces South America and the West Indian Islands, is almost equally primitive and weak, possessing only ancient and simple forms of life. It possesses, towards its southern extremity, the haplogonous group *Amphidoxa*, and the protogonous genus *Polygyratia*, which attest the ancient character of its mollusks, the simpler forms of the more modern dart-bearers having only penetrated as far as its northern parts and to the islands of the Greater Antilles.

The region exhibits its relationship with South Africa and Australasia by retaining a preponderance of the simply organized groups which at one period overspread the whole surface of the globe, but appear to have only differentiated externally in the size, shape and general character of the shell in response to the varying character of the environment they encountered in the course of their great migrations, the internal organization preserving in the main its original or primitive simplicity.

The West Indian islands exhibit all the peculiarities of pronounced insularity, displaying a remarkable individuality in the preservation of a marvellous development of Operculates and of a primitive section of Epiphallogonous Helices, reproducing in an analogous way the same characteristic association of those groups as is found in the Indo-Malayan region, and although the Helices are morphologically low, they are yet in advance of the Protogonous species characterizing the Atlantic and Gulf States of North America.

The Oriental region includes India, Further India and the islands adjacent to the equator; it is bounded on the north by the

Himalayas and by the southern watershed of the Yang-tse-Kiang, meeting with the Pacific near Shanghai; the west boundary is formed by the desert lands of North-West India and South Central Asia.

This region is distinguished malacologically by the great development of Operculates and the predominance of the Epiphallogonous group of Helices, peculiarities shared with the West Indian Islands.

The Ethiopian region includes Southern Arabia, all Africa south of the Sahara, and the Malagasian sub-region. Its fauna is of a very lowly stamp, especially in its extreme southern part and in the subsidiary island of Madagascar, the characteristic mollusks showing a remarkable affinity with those of Australia and other primitive regions.

The Arctic region is circumpolar and extends from the Arctic ocean on the north to the limits of the Nearctic and Palæarctic regions respectively, and although possessing so limited a fauna, it cannot well be treated otherwise than as a distinct region, as the Palæarctic and Nearctic regions have each a Helicidian fauna of a radically different stamp, the Euadenia being dominant in the latter region, while in the former they are decidedly a waning race.

Although the fauna of this region is restricted chiefly to freshwater races and to Helices and other genera of small size, capable of resisting a rigorous climate, possibly diffused throughout the Canadian region of North America by migration from Northern Europe, over the assumed ancient Pliocene connection by way of Greenland; the fauna is yet in a measure comparable with the Mongolian fauna, as the region is occupied in great part by the weaker terrestrial species thrust aside by the tide of stronger forms advancing from the European sub-region across Central Asia along the more fertile tract of country north of the desert region.

The freshwater species, however, inhabiting the extensive and connected lake region of boreal North America, will, from the keener competition they necessarily contend against, tend naturally to become more dominant than individuals, even of the same species, confined to more restricted and less competitive areas.

The Nearctic region embraces the continent of North America, south of the Arctic region, and may be divided into three sub-regions: Californian, Central and Alleghanian, but owing to the insuperable obstacle to the ready migration of the stronger races presented by the mountain ranges which bisect the continent from north to south there is a great inequality in the vigour of the occupants of the different

regions, for while in the Californian sub-region we meet with a preponderance of comparatively highly organized belogonous species, comparable with those of Japan and China, the more remote eastern slope, or Alleghanian sub-region, chiefly displays fine and numerous representatives of primitive protogonous types, comparable to those of South Africa, South America or Australia, while the arid Central sub-region is characterized by the possession of large examples of the even more archaic Haplogonous Helicoids.

The PALÆARCTIC region, as restricted, is the largest of the zoological divisions, and extends from the southern limit of the Arctic zone on the north to the Himalayas and the Sahara in the south, and embraces the whole extent of the Eastern Hemisphere from the Atlantic to the Pacific.

To express the differences in the character of the fauna, this enormous tract of country has been divided into three sub-regions: Mongolian, Mediterranean, and European.

The MONGOLIAN sub-region embraces the bleak and barren wastes of Tartary and the elevated mountain regions of Central Asia, including the district around Lake Baikal, which retains so many archaic forms of molluscan life. The more arid parts of the sub-region are occupied chiefly by the weaker Xerophiloid forms, characterized by whitish coloration and distinct sculpture, while the more fertile country further to the north is occupied by Fruticiculoid forms, allied to those of Europe, the whole fauna being more nearly related to the North American fauna or to the European post-tertiary deposits, rather than to the existing fauna of middle Europe.

The MEDITERRANEAN sub-region includes the countries encircling the Mediterranean Sea and extends eastwardly to Persia and Afghanistan, and is separated from the stronger North Central European region by the interposition of great mountain chains, which are a powerful obstacle to the rapid diffusion of improved races; this sub-region is characterized by the development of the relatively simple species of the genera *Campylæa*, *Helicella*, etc., which show a wealth of species within this area, and also retains within its limits many more species less advanced in development than are found within the area of the more vigorous North Central sub-region.

The EUROPEAN sub-region is bounded on the south by the mountain chains which separate it from the Mediterranean region, on the north by the southern boundary of the arctic region, on the west by the

ZOO-GEOGRAPHICAL REGIONS OF THE GLOBE

(modified after Wallace).

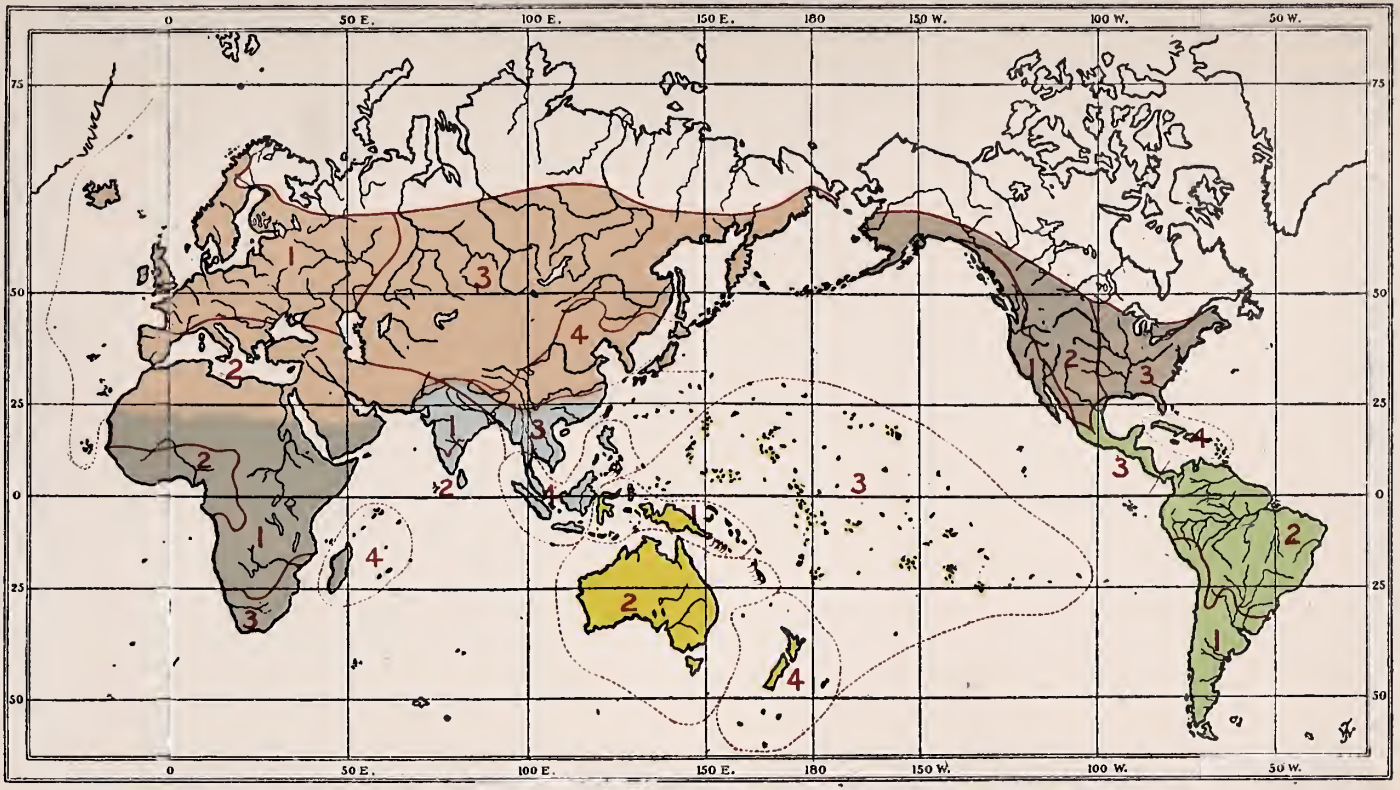


PLATE V.

WHITE indicates the Arctic faunal realm; RED, the Palæarctic region, 1 European sub-region, 2 Mediterranean, 3 Siberian, 4 Mongolian; PURPLE, the Nearctic region, 1 Californian, 2 Central, 3 Alleghanian; GREEN, the Neotropical region, 1 Patagonian, 2 Brazilian, 3 Mexican, 4 Antillean; BLUE, the Oriental region, 1 Indian, 2 Cinghalese, 3 Indo-Chinese, 4 Malayan; PURPLE, the Ethiopian region, 1 Mid-African, 2 West African, 3 South African, 4 Malagasian; YELLOW, Australasian region, 1 Papuan, 2 Australian, 3 Polynesian, 4 Maorian.

Atlantic, and on the east by the Ural Mountains and the Caucasus. The characteristic Helicine inhabitants are undoubtedly the Pentatænia, a group embracing our familiar species *Helix aspersa*, *Helix nemoralis*, etc., which are the most highly organized Helices upon the globe, and possess a pre-eminent power of adaptability to novel conditions and an ability to prosper under comparatively unfavourable conditions. Although it is probable that the tertiary molluscan remains are usually correctly referable to the groups still inhabiting their respective districts, yet in this sub-region the strata of more ancient periods would, if preserved, probably display relics of more generalized types from which the widely distributed and more primitive groups have been derived.

The British Isles belong to the European sub-region, and their molluscan fauna has been derived therefrom prior to the formation of the English Channel, when there was an actual connection at one or more points, the early isolation of this country doubtless contributing in some degree to the paucity of our fauna in comparison with that of the continent, although had the connection still existed we must still have looked for diminished numbers of species and individuals as we approach the north and become more remote from the centre of dispersion.

The total number of terrestrial mollusca inhabiting these islands is 127, of which 82 are land shells and 45 freshwater; of this number Ireland possesses 105 species, of which 69 are land and 36 freshwater shells. Its early separation from Great Britain has prevented the influx of a few other species which exist in the north-western counties of England. Scotland, though continuous with England, has not favourable geological or physical features, and its geographical extension northwards also acts prejudicially upon the development and extension of many forms of molluscan life, so that we find only 102 species resident therein, of which 68 are land and 34 freshwater, and these are mostly restricted to its more southern parts.

The present fauna of these isles consists of a number of more or less archaic or simpler forms and a series of improved or stronger races or species, these becoming evolved by the competition and struggles for existence continually taking place, more especially in the extensive, densely inhabited and therefore more competitive areas, and with the more highly developed organisms—the stronger races which arise being more exactly adapted to the environment and also

more adaptable to its modifications than their weaker predecessors, gradually overcome or dispossess them of the more favourable regions, starving out and driving the previous possessors to remote areas or compelling them to take refuge in the less desirable districts to which their range becomes more and more restricted and consequently isolated.

Viewed in regard to its mollusca, the British Isles may be divided into a Western or Celtic and an Eastern or Teutonic province; and although these districts cannot be rigorously defined, as some species have advanced beyond their fellows, while others, owing to later advent or greater susceptibility to changes of environment have not advanced so far, yet they undoubtedly express the salient feature of our molluscan fauna and its connection with the general scheme of distribution.

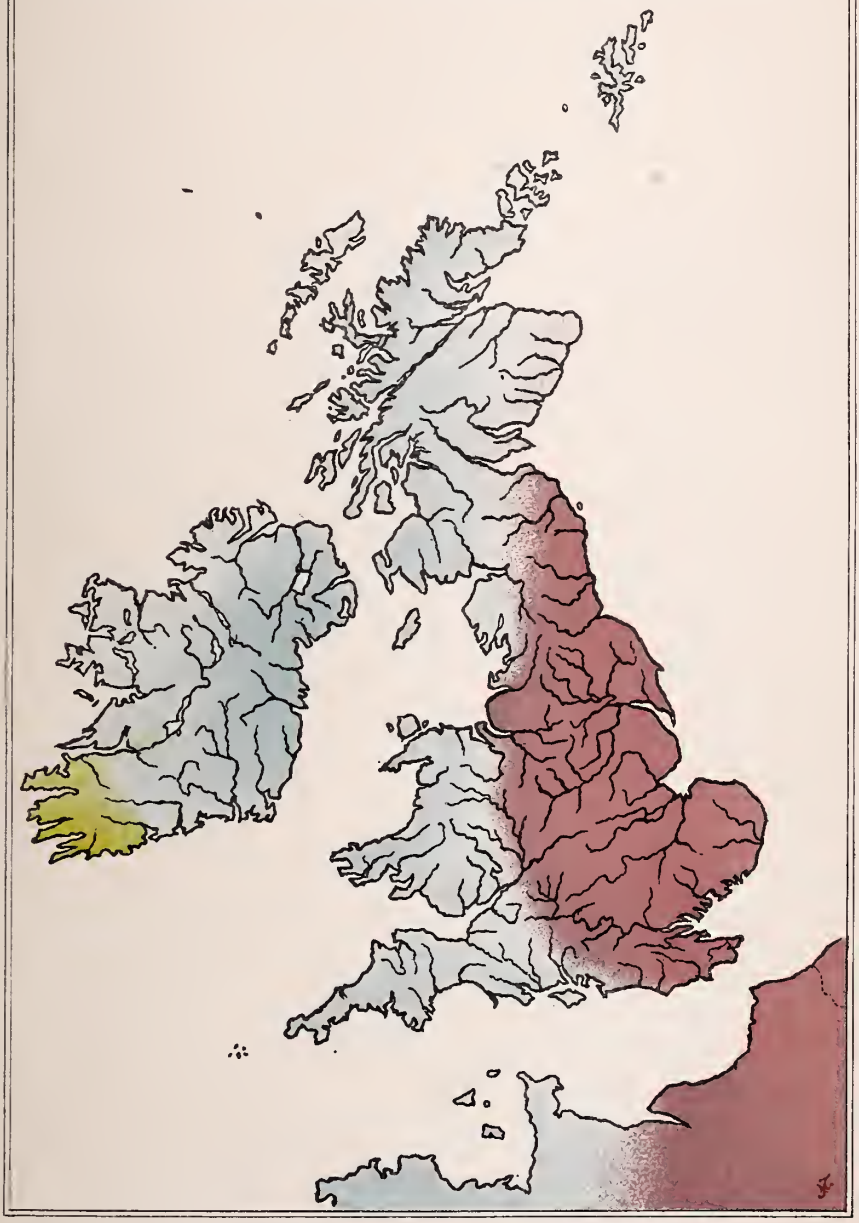
The WESTERN or Celtic province comprises the whole of Ireland and the western portions of England, Scotland and Wales as delimited, its characteristic feature consisting of the presence of a number of weaker species, whose originally conterminous areas of occupation have been cleft in twain by their more or less complete expulsion from the South-Eastern and Midland districts of England by the advancing general body of improved species, as although the later developed Pentatæniate species have outstripped their less highly organized brethren and overspread the whole of the British Isles, this is due to their marked superiority to the bulk of our fauna in organization and adaptability.

Probably the oldest, as it is also geographically the most remote section of this Western fauna, comprises the peculiar forms of life occupying the extreme south-west of Ireland, many of whose component species are also found inhabiting the west of the Iberian peninsula; these forms, represented among the mollusca by *Geomalacus maculosus*, are not improbably on the verge of extinction, being now reduced to and confined within these restricted districts by the pressure of the more highly organized forms of life which have already driven them from the more easterly tracts which they probably formerly inhabited, and are now gradually invading and dispossessing them of the territory upon which they still linger.

The older notion, which regards as the original home of a primitive species the districts wherein it now exists, is in my view manifestly inaccurate, and we must regard the regions now occupied by weaker groups as one of the various stages of their retreat before the advance

FAUNAL MAP OF THE BRITISH ISLES.

The RED area approximately represents the province inhabited by the advancing Teutonic races; the BLUE that of the retreating Celtic races; the YELLOW sub-area indicates the district in which the disappearing so-called Lusitanian forms still linger.



of the improved and improving races, which invade this country in such a way as tends to divide its previous occupants into a northern and a southern section, as exemplified by the distribution of *Unio margaritifer*, *Pupa anglica* and other species ; the northern section being driven towards the north, and not spreading or having spread southward as is the prevalent belief.

This waning western fauna is exemplified by *Helix fusca*, *Helix lamellata*, *Pupa anglica*, *Succinea oblonga*, *Unio margaritifer*, etc.

The Eastern or Teutonic province, which embraces the whole eastern districts of Britain, consists chiefly of the more highly organized and later immigrant species, which have invaded our South-Eastern shores and advanced mainly in a westerly and north-westerly direction, driving before them the feebler western species and gradually isolating them or restricting the area they inhabit to Ireland and to the southern or northern extremities of Britain. In Ireland there is a less severe competition, owing to the later advent and limited number of the more vigorous eastern types, so that many weaker species are still flourishing, although the feeble remnant of the Iberian molluscan fauna, now restricted to narrow limits in the more remote south-western district, is on the point of extinction.

Among these more dominant eastern species may be enumerated *Helix nemoralis*, *H. aspersa*, *H. pomatia*, *Pupa secale*, *Planorbis corneus*, *Limnæa peregra*, *Unio pictorum*, etc.

The Geological history or distribution in time of the mollusca, forcibly displays the operation of the same laws as govern their distribution in space, furnishing evidence by their fossil remains, not only of the successive evolution of new forms, but also of the eventual extinction or gradual expulsion from the vicinity of the evolutionary area by the more vigorous and later developed species of the weaker and more primitive previous inhabitants.

Many of these weaker forms, however, still survive, their survival being probably due to the adoption of dissimilar habits or foods to those of the more dominant species among which they live, others though locally extinct, still exist in other regions, finding a respite from their inevitable and impending extinction by continual retreat to more and more distant regions before the advancing hosts of improved forms.

Many of the older rocks have lost all traces of the fossils they undoubtedly originally contained and this obliteration of the precious relics of a byegone life, leaves us, so far as direct evidence is con-

cerned, in a state of helpless uncertainty as to the character of the more primitive life forms. Most strata also are of marine origin, and fossilized land and freshwater species are naturally seldom met with.

Fossil, though meaning anything dug out of the ground, is restricted to the relics of organized life entombed in the rocks; the term Subfossil being usually applied to them when found in beds at present in course of deposition. Conchologically a fossil may be the actual shell itself not noticeably altered, or the shell substance may have perished, owing to the percolating water having dissolved and carried away in solution the carbonate of lime of which it is composed, and which as dissolved may be replaced by a deposit of silica or other substance, sometimes preserving not only the external form and appearance, but even in great part the internal structure, or the cast or impression only, may be left, which, however, may exhibit every peculiarity or detail of the original shell with minute accuracy.

All rocks containing fossils are stratified and, except those of calcareous composition, are mainly formed by aqueously deposited layers of mud, sand, or other material derived from the waste of the land, and although the first or earliest stratified deposits were necessarily formed from the disintegration of the igneous rocks, yet subsequent beds are formed in great part from the waste of previously formed strata which have become elevated above the water level, and in this way the same material has been worn away by atmospheric forces and redeposited elsewhere, and as this may have occurred again and again the destruction and loss of their fossil contents is almost assured, for as soon as dry land is formed it is immediately acted upon by rain, frost and other atmospheric agents, and the consequent erosion and denudation provides the sediment for the formation of the new rocks, which are deposited in layers or strata, a succession of which more or less similar in character is called a Formation.

The formations are grouped together in three great divisions, known as the Primary, the Secondary and the Tertiary periods or Systems.

The Palæozoic (παλαιός, old ; ζῶή, life) or Primary system embraces the Archæan, Cambrian, Silurian, Devonian, and Carboniferous series of rocks, and is remarkable for the marvellous development of the Trilobites, an extinct group of Crustacea, restricted to the Palæozoic era, which attained its maximum about the close of the Cambrian period. It is also characterized by the presence of holostomatous Gastropods, although the Pelecypods preponderate in numbers.

The Cambrian rocks in this country are enormously developed, probably being not less than five miles in thickness; they rest unconformably on the still more ancient Archæan rocks, which have lost all traces of the organisms that in all probability lived during the period of their deposition, so that the relics of the organized life of the Cambrian period are the earliest of which we have cognizance in this country, but we find therein well organized representatives of all the classes of mollusca, and we must, therefore, look immeasurable ages further back for the ancestral form from which they originally diverged, all traces of which have been obliterated by the excessive denudation and changes which the earlier strata have undergone.

No representatives of land and freshwater genera are recognized in Cambrian strata, but, as those groups are directly derived from marine species, it is probable that the earlier forms would retain for a time a marine facies and not be readily separated from the truly marine species from which they originated.

The Devonian rocks are well distributed over the British Isles, and, with the exception of strata found in Devon and Cornwall, are probably mainly of fresh-water origin and known as the Old Red Sandstone, the colouring of the strata being due to iron oxides. This formation is remarkable for the discovery at St. John's, New Brunswick, of the earliest known Pulmonate, *Pupa primæva*, and in this country for the appearance of

Archanodon jukesi Baily,

a species scarcely distinguishable externally from the ordinary *Anodonta* of our own day, and the first undoubted representative of our fresh-water fauna, which has been found near Cork, at Kiltorkan and Tallow Bridge in county Waterford; near Caerleon in Monmouth, and in Northumberland.

The Carboniferous system is so called because it contains the chief coal deposits, known as the Coal measures, which are as much as 10,000 feet thick in South Wales. Conchologically, this deposit is remarkable for the discovery in the South Joggins Coal-field, Nova Scotia, of a number of terrestrial Pulmonate species referable to various genera, and in this country for the appearance of a wealth of species of primitive Unionidæ and Mytilidæ, classified as *Carbonicola*, *Anthracomya*, and *Naiadites*.

The *Carbonicola* and *Anthracomya* are Unioniform genera, differing from the modern Uniones in the dorsal and posterior position of the

accessory anterior pedal scars. The *Anthracomya* differ from *Carbonicola* by possessing a broadly expanded and truncate posterior region and a well-defined gonial ridge.

The *Naiadites* are inequivalve Mytiloid forms, characterized by the anteriorly directed and subterminal umbones, and externally resembling *Dreissensia* in shape and ornamentation as well as in the distinct presence of the byssal notch.

The fossils of this formation are :—

UNIONIDÆ.

Carbonicola acuta (J. Sow.),
— v. *rhomboidalis* Hind,
angulata (Ryckholt),
antiqua Hind,
aquilina (J. de C. Sow.),
cuneiformis Hind,
elegans (Kirkby),
gibbosa Hind,
inæqualis Hind,
obtusa Hind,
ovalis (Martin),
polmontensis (Brown),
robusta (J. de C. Sow.),
rugosa (Brown),
similis (Brown),
subconstricta (J. Sow.),
subrotunda (Brown),
turgida (Brown),
riuti (Kirkby),
Anthracomya adamsi Salter,
— v. *expansa* Hind,
calvifera Hind,
dolobrata (J. de C. Sow.),
lanceolata Hind,
lævis v. *scotica* Etheridge jr.,
Anthracomya minima (Ludwig),
— v. *carinata* Hind,
modiolaris (J. de C. Sow.),
— v. *curtata* (Brown),
oboratu Hind,
phillipsi (Williamson),
pulchra Hind,
pumila Salter,
senex Salter,
subcentralis Salter,
subparallela (Portlock),
valenciensis Hind,
wardi Etheridge,
williamsoni (Brown),
— v. *obtusa* (Ludwig).

MYTILIDÆ.

Naiadites carinata (J. de C. Sow.),
— v. *tumida* Hind,
crassa (Fleming),
— v. *modioliformis* (Brown),
elongata Hind,
magna Hind,
modiolaris (J. de C. Sow.),
obesa (Etheridge jr.),
quadrata (J. de C. Sow.),
triangularis (J. de C. Sow.).

The MESOZOIC (μέσος, middle ; ζωή, life) or Secondary strata include the Trias, the Jurassic and the Cretaceous formations, and are characterized by the predominating development of the Pelecypoda and also contain fossil remains of genera long extinct in this country, but still flourishing in lands more distant from the evolutionary centre.

The *Melaniadæ*, which now characterize the Malayan peninsula, the African Continent, and are also numerous in Eastern North America and other primitive regions, were formerly abundant in this country, as testified by their remains in the Oolite, the Cretaceous and succeeding strata. *Corbicula* and *Unio* were also numerous in the secondary rocks, but the former is no longer found in this country, but restricted to distant areas, and the latter have now but three representatives, although in Eastern North America they abound at the present day. *Neritina*, *Vivipara*, and *Valvata*, are all archaic

forms represented in oolitic strata, and are now restricted in this country to very few representatives.

The Triassic system is not so well displayed in this country as in Germany, where the deposits are readily divisible into three sections, from whence arose the distinguishing name. It is mainly a marine formation, and characterized by the advent of siphonated Streptoneura, but otherwise resembling the Palæozoic era, as we know of no undoubted fossils of terrestrial mollusks therefrom in England. In its faunal aspect this formation has been compared to New Zealand and Madagascar at a comparatively recent period.

The Jurassic system receives its name from the Jura mountains, where it is well displayed; it shows a prevalence of the siphonated gastropods and also the advent of the Opisthobranchiate forms. It embraces the Lias and the Oolitic formations and has been considered by Phillips to represent the organic aspect of Australia at the present day.

The Lias, apparently a quarryman's corruption of layers, is remarkable for the appearance of the Ammonites, which quickly attain a most remarkable development, and in this country for the advent of certain well differentiated genera of pulmoniferous Gastropods, not previously recognized in British strata. The known species recorded from liassic strata are :

HELICIDÆ.
Helix dawsoni Moore.
PUPIDÆ.
Vertigo murchisonæ Moore.
LIMNÆIDÆ.
Planorbis mendipensis Moore.
PALUDESTRINIDÆ.
Paludestrina solidula (Dunker).
VALVATIDÆ.
Valvata anomala Moore,
pygmea Moore.
DESPŒNIDÆ.
Despœna lyelli (Moore).
NERITIDÆ.
Neritina arenacea Terq.,
canalis Terq.,
hettangiensis Terq.

The Oolites (ὠόν, egg ; λίθος, stone), so named on account of consisting of a mass of small rounded egg-like particles, are according to the classification adopted in England, divided into three sections: the Lower Oolites, the Middle Oolites, and the Upper Oolites, and are remarkable as containing in the Bavarian deposits the remains of the oldest-known bird, the *Archæopteryx macrura*.

The Lower Oolites embrace the Inferior Oolite, the Great Oolite, and Cornbrash. The Stonefield Slate occurs at the base of the Great Oolite; its fossil remains show that the life of the period greatly resembled that of Australia at the present day, where marsupials, sharks cycads, and pines still flourish.

The Lower Oolites display the advent of the genera *Melania* and *Corbicula*, unknown in earlier formations in England, comprising representatives as enumerated :

MELANIIDÆ.
Melania inermis Tate,
Leptoxis trochiformis Tate.

PALUDESTRINIDÆ.
Paludestrina caledonica (Tate),
præcursor (Sandberger).

VIVIPARIDÆ.
Vivipara langtonensis (Hudleston),
scotica (Tate).

VALVATIDÆ.
Valvata comes Hudleston,
præcursor Tate.

NERITIDÆ.
Neritina arata Tate,
staffinensis Forbes.

UNIONIDÆ.
Unio distortus Bean,
staffinensis Forbes.

CORBICULIDÆ.
Corbicula arata (Forbes),
brycei (Tate),
cucullata (Tate),
cunninghami (Forbes),
jamesoni (Forbes),
macculloch (Forbes).

The Middle Oolites embrace the Kelloway Rock, Oxford Clay, and Coral Rag, and exhibit no terrestrial or fluviatile fossil remains.

The Upper Oolites include the Kimmeridge Clay, Portland Limestone, and the Purbeck beds; the latter strata display a prevalence of freshwater conditions, the grey freshwater limestones so characteristic of this formation known as Purbeck marble, which was so largely used by mediæval architects for the interior ornamental parts of ecclesiastical edifices, being almost entirely made up of fossilized *Vivipara*, the *Vivipara elongata* being the predominant species. The deposits also show an increase in the *Melaniidæ*, while *Physa* makes its appearance.

The land and freshwater fossils of this epoch embrace the following species :—

LIMNÆIDÆ.
Limnæa physoides Fisher,
Physa bristovi Lyell,
wealdiana Coquand,
Planorbis fisheri Forbes.

MELANIIDÆ.
Melania popei (J. de C. Sow.),
Melanopsis attenuata J. de C. Sow.,
harpæformis Dunker,
popei J. de C. Sow.,
rugosa Dunker,
tricarinata J. de C. Sow.

VALVATIDÆ.
Valvata helicoides Forbes.

VIVIPARIDÆ.
Vivipara carinifera (J. de C. Sow.),
elongata (J. de C. Sow.),
sussexiensis (Mantell).

UNIONIDÆ.
Unio compressus J. de C. Sow.,
valdensis Mantell,
Anodonta purbeckensis Morris.

CORBICULIDÆ.
Corbicula angulata (J. de C. Sow.),
elongata (J. de C. Sow.),
gibbosa (J. de C. Sow.),
media (J. de C. Sow.),
membranacea (J. de C. Sow.).

The CRETACEOUS (creta, chalk) system, which terminates the Mesozoic period, is named from the chalk which constitute its most characteristic strata, the freshwater deposits of the lower division are known as the Wealden, from their best development being in the Weald, the formation is considered to be probably derived from the accumulations, either in a lake or in an estuary of the detritus of a

great river flowing from the north-east. The Weald clay is of a pale grey and is near 1,000 feet thick and contains bands of shelly limestone, known as Petworth marble, which are thickly studded with fossils of *Vivipara*, chiefly *Vivipara fluviorum* Sowerby. The fossils are distinctly freshwater species and embrace *Vivipara, Unio, Melanopsis, Corbicula*, etc.

In North America, where more favourable conditions existed at this period for the preservation of fossil remains, many subgeneric groups flourishing at the present day are found to have lived as early as the close of the cretaceous epoch. *Acella, Limnophysa, Gyraulus, Bathyomphalus, Aplecta, Physa*, and other subgenera of *Limnæidæ* are distinctly represented in the Laramie and other strata. The *Helicidæ* were almost as diversified as at the present day, forms apparently referable to *Aglaia, Epiphragmophora, Strobila, Pyramidula, Triodopsis*, etc., being found, while the *Unionidæ* showed also a remarkable differentiation, as subordinate types largely identical with many still Mississippian, even then existed, though many living types had apparently no living representatives at that period.

The known British fossils of this era are:

MELANIIDÆ.
Melania popei (J. de C. Sow.),
Melanopsis attenuata J. de C. Sow.,
popei J. de C. Sow.,
tricarinata J. de C. Sow.

VIVIPARIDÆ.
Vivipara carinifera (J. de C. Sow.),
elongata (J. de C. Sow.),
fluviorum (J. de C. Sow.),
sussexiensis (Mantell).

NERITIDÆ.
Neritina fittoni Mantell.

UNIONIDÆ.
Unio aduncus J. de C. Sow.,
antiquus J. de C. Sow.,
compressus J. de C. Sow.,

UNIONIDÆ.
Unio cordiformis J. de C. Sow.,
gualtieri J. de C. Sow.,
mantelli J. de C. Sow.,
martini J. de C. Sow.,
porrectus J. de C. Sow.,
subtruncatus J. de C. Sow.,
valdensis Mantell.

CORBICULIDÆ.
Corbicula angulata (J. de C. Sow.),
elongata (J. de C. Sow.),
gibbosa (J. de C. Sow.),
major (J. de C. Sow.),
media (J. de C. Sow.),
membranacea (J. de C. Sow.),
subquadrata (J. de C. Sow.).

The TERTIARY period opens with the elevation of the greater part of the British Isles above the sea, which were therefore subjected to the unavoidable denudation and waste of surface that would furnish the material for the formation of rocks elsewhere, instead of being more or less submerged and receiving deposits from the waste of other lands; an interval thus exists between the lower tertiary beds and the cretaceous strata, and the lapse of time this gap represents must have been enormous, as with perhaps one or two exceptions all the cretaceous species have disappeared, before the deposition of the lowest tertiary beds, and this is the more remarkable as the number

of known species has in the interval become nearly double in number. On the Continent, however, this great break in the succession of strata is not nearly so marked, and in North America the series connecting the two formations is fairly represented by the Laramie formation.

This period in this country embraces three groups of strata, the Eocene, the Oligocene, and the Pliocene formations, the predominating development of the Gastropoda being the most remarkable feature of the period, but also showing a much more decided approximation to the present inhabitants of our country generally, the proportion of living to extinct species increasing from perhaps 5% in the Eocene to 75% or more in the later deposits.

Few remains of our present species are found earlier than the Eocene beds of the Tertiary period, and in this country many strata, which would probably have yielded large numbers of fossils, have been swept away by the extensive denudations extending over vast ages of time, so that not even fragmentary relics are now available for study.

The EOCENE (ἠώς, dawn; καινός, recent) is the oldest of the tertiary group, its deposits chiefly occupying two great depressions in the chalk, known as the London and Hampshire basins, and being considered to show the origin or dawn of the present fauna of the earth, as its beds contain remains of genera which although now exterminated in this country, still exist in closely-related forms in the more remote regions of the globe, showing that a different geographical distribution of organisms from the present existed in former times. Many genera of mollusca which were in Eocene times inhabitants of this country are now restricted to other and distant climes, as *Amphidromus* which is now found chiefly in the Indo-Malayan region, *Camptoceras* now confined to India, etc.

The following are the known species from this formation :—

BULIMULIDÆ.

Amphidromus rillyensis (Boissy).
tenuistriatus (Sow.).

PUPIDÆ.

Megaspira cylindrica Newt. & Harris.

LIMNÆIDÆ.

Limnæa cylindrica Newton & Harris,
Pitharella rickmani Edwards,
Planorbis cuampladus J. Sow.,
hemistoma J. Sow.,
incertus Newton & Harris,
lævigatus Desh.,
Camptoceras priscum Godwin-Austen,
— v. *obtusa* Godwin-Austen,

AURICULIDÆ.

Pedipes glaber Edwards.

MELANIIDÆ.

Melania heyscana Philippi.
Melanopsis ancillarioides Deshayes,
buccinoidea Fér.,
buccinulum Deshayes,
carinata J. de C. Sow.,
microstoma Edwards MS.,
pseudo-subulata Newton,
sodalis Desh.,
Melanatria ignota Edwards MS.,
inquinata (Defrance),
vulcanica (Schloth).

MELANIIDÆ.
Coptostylus globosus Edwards MS.

PALUDESTRINIDÆ.
Paludestrina ambigua Edwds. MS.,
subpulchra Edwards MS.,
Tomichia microstoma (Deshayes),
teres Edwards MS.,
tuba (Deshayes),
Pyrgula pulchra (Raincourt),
Bithynella websteri (Morris),
Stenothyra parkinsoni (Morris).

VIVIPARIDÆ.
Vivipara aspersa (Michaud),
lenta (Solander).

NERITIDÆ.
Neritina consobrina Fér.,
globulus (Fér.),
passyana Desh.,
vicina Melleville,
— v. *jaspidea* Desh.

UNIONIDÆ.
Unio edwardsi S. V. Wood,
michaudi Desh.

UNIONIDÆ.
Unio subparallela S. V. Wood.

CORBICULIDÆ.
Corbicula aduneа (Edwards MS.),
altirupestris (Edwards MS.),
anceps (S. V. Wood),
britannica (Desh.),
charpentieri (Potiez & Michaud),
cordata (Morris),
crassa (Deshayes),
cuneiformis (J. Sow.),
deperdita (Lamarck),
dulwichiensis (Rickman),
forbesi (Deshayes),
intermedia (Melleville),
obovata (J. Sow.),
pullastra (S. V. Wood),
sororcula (Edwards MS.),
strigosa (S. V. Wood),
subdepressa (Edwards MS.),
tellinella (Fér.),
trigona (Desh.),
tumida (S. V. Wood).

The OLIGOCENE (ὀλίγος, few; καινός, recent) the fluvio-marine series of Forbes, is considered to be the representative of the early stages of the Miocene period in the British Isles; it shows a still closer approximation to the present fauna than that of the preceding strata, its remains possessing so great an interest and beauty that a short summary of the situation and character of the different beds is given. Its deposits consist of marls, sands, clays, and limestones, and are confined to the Isle of Wight and to Hampshire, the estuarine and freshwater conditions under which the strata were mainly deposited being shown by the abundance of *Cerithium*, *Potamomya*, *Corbicula*, *Limnæa*, etc.

The Oligocene deposits are subdivided into four chief beds, designated by the names of the localities where they are well displayed: the Headon, the Osborne, the Bembridge, and the Hempstead beds.

The Headon series are exhibited at Totlands and Colwell Bays and Headon Hill, *Planorbis euomphalus* Sow. being the characteristic fossil of the series. The beds may be subdivided into an upper, a middle, and a lower series. The middle Headon is mainly marine or brackish. The lower series is composed of clays and marls with intercalated beds of freshwater limestone, and is also displayed at Hordwell Cliffs in Hampshire. The upper Headon is freshwater, and shows characteristic Limnæan limestones, shales, and marls.

The Osborne series is visible at St. Helens, Osborne, Headon Hill, Colwell, Totlands, and Gurnet Bays.

The Bembridge series, of which *Planorbis discus* Edwards is perhaps the most characteristic fossil, is exhibited in the cliffs of Whitecliff Bay, along the shore and low cliffs under Hempstead Hill, at Sconce, at the crest of Headon, and at a few inland limestone quarries.

The series of freshwater marls are separated by a marine bed from the limestone band which contains terrestrial pulmonate remains as well as fossilized *Viviparæ*, *Planorbes*, and *Limnææ*.

The Hempstead beds are the uppermost of the series and have been almost obliterated by the enormous amount of denudation to which they have been subjected, the only remnants of this series being at Hempstead Hill, near Yarmouth, Isle of Wight. They are constituted by clay and shaly marls, and were deposited under alternating marine and fluviatile conditions.

The fossil remains from the Oligocene beds are very numerous and comprise :

TESTACELLIDÆ.

Glandina brevis Edwards MS.,
convexa (S. V. Wood),
costellata (J. Sow.),
— v. *abbreviata* (Edwards).

HELICIDÆ.

Hyalinia d'urbani (Edwards),
leia (Newton & Harris),
sconciensis (Newton & Harris),
Helix etheridgei Edwards MS.,
headonensis Edwards,
morrisi S. V. Wood,
occlusa Edwards,
omphalus Edwards,
pseudo-globosa Orbigny,
pseudo-labyrinthica Sandberger,
sublabyrinthica (Edwards),
tropifera Edwards,
vectiensis Edwards.

BULIMULIDÆ.

Amphidromus ellipticus (J. Sow.),
lævolongus (Boubée),

PUPIDÆ.

Pupa oryza Edwards,
multispirata Newton & Harris,
perdentata Edwards,
vectiensis Edwards MS.,
Vertigo dubia (Newton & Harris),
Clausilia striatula Edwards,
Megaspira monodonta Newt. & Harris,

STENOGYRIDÆ.

Achatina cylindrica Edwards MS.,
Zua headonensis (Newton & Harris),

SUCCINEIDÆ.

Succinea edwardsi Forbes,
imperspicua Edwards,
perspicua S. V. Wood,
sparnacensis Deshayes,

LIMNÆIDÆ.

Limnæa angusta Edwards,
arenularia Desh.,
caudata Edwards,
— v. *abbreviata* Edwards,
cincta Edwards,
columellaris J. de C. Sow.,
convexa Edwards,
costellata Edwards,
fabula Brongniart,
fusiformis J. Sow.,
— v. *deformis* Edwards,
gibbosula Edwards,
headonensis Newton & Harris,
longiscata Brongniart,
— v. *distorta* Edwards,
— v. *elongata* de Serres,
minima J. Sow.,
mixta Edwards,
ovum Brongniart,
pyramidalis Brongniart,
recta Edwards,
sublata Edwards,
subquadrata Edwards,
sulcata Edwards,
tenuis Edwards,
tumida Edwards,
Segmentina obtusa (J. Sow.),
Planorbis biangulatus Edwards,
discus Edwards,
elegans Edwards,
euomphalus J. Sow.,
goniobasis (Sandberger),
hemistoma J. Sow.,
lens Brongniart,
oligyratus Edwards,
platystoma Edwards,
sowerbyi Bronn,
tropis Edwards,

LIMNÆIDÆ.
Ancylus (?) *latus* Edwards,
Velletia elegans (J. de C. Sow.),
MELANIIDÆ.
Melania acuta (J. Sow.),
— v. *excavata* Morris,
— v. *tumescens* Edwds. MS.,
contabulata Edwds. MS.,
nysti Nyst,
Melanopsis carinata J. de C. Sow.,
fusiformis J. Sow.,
pseudo-subulata Newton,
subcarinata Morris,
subulata J. Sow.,
Coptostylus brevis (J. de C. Sow.),
PALUDESTRINIDÆ.
Paludestrina anceps Edwards MS.,
dubuissoni (Bouillet),
inflata (St. Fond),
peracuta Edwards MS.,
subangulata Edwards MS.,
Tomichia duchasteli (Nyst),
polita (Edwards),
Pyrgula ditropis Edwards MS.,
pulchra (Raincourt),
— v. *denticulata* Edwds. MS.
Bithynella pulchra (Desh.),
Stenothyra lubricella (Braun),
mediana (Deshayes),
parvula (Morris),
pupa (Nyst),
RISSOIDÆ.
Potamaclis forbesi (Morris),
peracuminata (Morris),
turritissima (Forbes),
woodi Edwards MS.,
VIVIPARIDÆ.
Vivipara angulosa (J. Sow.),
— v. *orbicularis* (Morris),
distinguenda (Deshayes),
globuloides (Forbes),
lenta (Solander),
vestita Edwards MS.,
CYCLOPHORIDÆ.
Dissostoma mumia (Lamarck),
Cyclotus cinctus Edwards,
nudus Edwards,
CYCLOPHORIDÆ.
Craspedopoma elizabethæ Edwards,
Pomatias heterostoma (Edwards),
minuta Edwards MS.,
rotundata Edwards MS.,
Callianella lævis (Sandberger),
DESPŒNIDÆ.
Despæna woodwardi Edwards MS.,
NERITIDÆ.
Neritina aperta (J. de C. Sow.),
— v. *zonula* S. V. Wood,
concava J. Sow.,
forbesi S. V. Wood,
fulminifera Sandberger,
planulata Sandberger,
tristis Forbes,
UNIONIDÆ.
Unio gibbsi Morris,
— v. *headonensis* S. V. Wood,
solandri J. de C. Sow.,
tumescens S. V. Wood,
vectensis S. V. Wood,
CORBICULIDÆ.
Sphærium bristovii (Morris),
tumidula (S. V. Wood).
headonense Edwards MS.,
morrisi Edwards MS.,
Corbicula æstuarina (Edwards MS.),
arenaria (S. V. Wood),
cycladiformis (Deshayes),
deperdita (Lamarck),
gibbosula (Morris),
mactræformis (Edwards MS.),
obliqua (Deshayes),
obovata (J. Sow.),
obtusa (Morris),
pisum (Deshayes),
pulchra (J. de C. Sow.),
— v. *wrighti* (Morris),
semistriata (Deshayes),
—v. *fortis* (Edwards MS.),
subregularis (Edwards MS.),
tenera (S. V. Wood),
transversa (Morris).
DREISSENSIIDÆ.
Dreissensia brardi (Brongniart).

The PLIOCENE (πλεῖον, more; καινός, recent) strata succeed the Oligocene in this country, as during the whole of the intervening Miocene period these islands were elevated above the sea, and probably united with the continent, but at the beginning of the Pliocene era the south-eastern districts were again submerged, and those various sand-banks and shell deposits were accumulated which constitute the 'Crag.'

The *Valvata antiqua* of Sowerby and related forms are now removed from the list of extinct Pliocene and Pleistocene species, as they are still found in this country in a living state.

The Coralline or White Crag, the most ancient of the East Anglian deposits, is composed of shelly sand and marls, the term coralline being due to the immense quantity of coral-like polyzoa it contains, many of which still retain the position they occupied when living.

The Red Crag is formed by local beds of dark-red or brown ferruginous sand, their colour being derived from iron oxides; they rest unconformably against and upon the White Crag. One of the most interesting shells of this formation is *Fusus contrarius*, a form closely allied to which still exists near Vigo Bay.

The Norwich or Mammalian Crag consist also of shelly sand and gravel, attaining in places a thickness of from 150 feet to 180 feet. The name is derived from one of the localities where the beds are well exposed, and the descriptive name is in allusion to the presence of bones of the Mastodon and other mammalia which are found in places at the base of the deposit.

The Pliocene fossils of species now extinct in the British Isles are :

HELICIDÆ.
Helix fruticum Müller,
lens Fér.,
lactea Müller,
incarnata Müller,
rubiginosa A. Schmidt,
rysa S. V. Wood,
suttonensis S. V. Wood,

PUPIDÆ.
Clausilia pliocena S. V. Wood,

PALUDESTRINIDÆ.
Paludestrina obtusa v. *reevei* K.&W.,
pendula S. V. Wood,
terebellata (Nyst),

VIVIPARIDÆ.
Vivipara glacialis (S. V. Wood),
media (S. Woodward),

CORBICULIDÆ.
Corbicula fluminalis (Müller).

The Post Tertiary strata may be considered as inaugurating a fourth or quaternary epoch, and as linking the life of the Pliocene period with that of the present day; its beds are composed of various superficial deposits in which all or nearly all the mollusca are recent species.

The geological history of our British species is in its origin still wrapped in obscurity, as the pleistocene remains though showing certain species now extinct in this country, exhibit also many of our present species, apparently as far as the shell enables us to judge, quite as sharply differentiated as at the present day, so that we must look far into the past before we can hope to meet with relics of the progenitors of the present molluscan fauna of our country, as we have no distinct traces left behind even of the various stages, as shown by the embryonic whorls, through which the present specialization and perfection of their shell structure has been acquired.

These, post tertiary beds may be separated into two groups, which are distinguished as Pleistocene and Holocene.

The Pleistocene (πλειστος, most; καινός, recent) Post Pliocene, Glacial, or Diluvial beds, as they are variously called, are rather few and fragmentary in this country, consisting only of such remnants as have escaped destruction by the enormous denudation to which its deposits have been subjected.

The pleistocene beds would appear to have been deposited during a gradual refrigeration of the climate, until what is known as the "Ice Age" prevailed, the condition of a great part of the British Isles being compared at this period to that of Greenland at the present day.

These deposits, also known as the Palæolithic age, are the first containing undoubted evidence of the existence of man, his presence at this period being attested by the discovery of the roughly chipped flint arrow-heads and other weapons and implements associated with remains of the mammoth, hippopotamus, rhinoceros, lions, bears, and other animals characteristic of the period in this country.

The Holocene (ὅλως, entirely; καινός, recent) or Post Glacial period, is composed of recent superficial deposits, river alluvia, peat moors, sand dunes, lacustrine deposits, etc., which contain no fossilized remains of species now extinct, the differences shown by the mollusca, compared with those existing at the present day in the same region, being now confined to variations, which although they may not now live in the British Isles, yet are still found in neighbouring countries. It is also known as the Neolithic age, the stone implements of the savage races of mankind living at this period being more highly finished than the ruder ones of the preglacial peoples.

The Post-Tertiary fossils now extinct in this country are:

LIMACIDÆ.
Limax modioliformis Sandberger,
HELICIDÆ.
Helix fruticum Müller,
nemoralis v. *creticola* Mörch,
ruderata Studer,
umbrosa Partsch,
PUPIDÆ.
Vertigo concinna Scott,
Clausilia pumila v. *sejuncta* Schmidt,
LIMNÆIDÆ.
Limnæa palustris aff. *diluviana* And.
VIVIPARIDÆ.
Vivipara clactonensis (S. V. Wood)
PALUDESTRINIDÆ.
Paludestrina marginata (Michaud),
Bithynella steeni (E. von Martens),
Bithynia ovatula Sandberger,
Nematurella runtoniana Sandberger,
UNIONIDÆ.
Unio littoralis Lamarck.
pictorum v. *limosa* Nils.
CORBICULIDÆ.
Sphærium corneum v. *mœnanum* Kob.
Corbicula fluminalis (Müller),
Pisidium amnicum v. *astartoides* (Sandberger).

The faunal changes which have taken place on the earth is shown by the preceding varying lists of the species obtained from the different geological formations. These changes in the molluscan fauna have their analogies or counterparts in the succession of life observed in all

other classes of the animal and vegetable kingdoms, displaying the unity of the plan for the diffusion of organic life over the globe and emphasizing the reality and truth of the extinction of the weaker and more primitive races or their expulsion from those countries adjacent to the evolutionary area by the later developed and more adaptable races as already described under geographical distribution.

The earlier deposits contain fossilized remains of species or genera wholly extinct at the present day or now living only in inclement regions or in countries far distant from the regions in which they formerly existed. In the later rocks the number of such forms steadily diminish, and the area of their present distribution becomes less and less distant from the creative centre, the species gradually approximating to, and eventually becoming absolutely identical with, the present inhabitants of the district where the fossilized remains are found.

The ENEMIES of the mollusca are very numerous, as they constitute a favourite and nourishing food for many animals, their defenceless condition and sluggish movements rendering them an easy prey to many creatures besides man, their only protection being the distastefulness of certain species, or their power of concealment, as their shell only affords protection against their weaker or less astute enemies.

The MAMMALIA are very destructive to the molluscan life, more especially during the oft-recurring periods of scarcity of their accustomed food.

The Rats in this country destroy and devour large numbers of *Helix aspersa*, *H. nemoralis*, etc., this being evidenced by the large number of their broken shells strewn about their holes; in winter, they laboriously dig up from their concealment in the ground the hybernating or æstivating mollusks, whose whereabouts they have detected, and have even been observed to ascend hollyhocks and other plants and bring down to their holes for food the *Helix aspersa* infesting them, the broken shells, the relics of the feast, being left strewn about their retreats.

In Australia the Bush Rat (*Mus arboricola* Macl.) shows the same predilection, and destroys large numbers of the *Helix aspersa* which live in the Botanic Gardens at Sydney, always accomplishing this purpose by breaking in at the apex of the shell.

The Voles generally, prey upon the mollusca, the Bank Vole evincing a predilection for *Helix fusca*, though also destroying other species.

Field-Mice also consume large quantities of mollusca, breaking into the shell by gnawing away the side of the whorl, and from the ascertained extent of their depredations and those of their congeners, the devastations of the mice must be a decided check upon molluscan increase. Included amongst the list of species preyed upon by these animals are *Helix cantiana*, *H. arbustorum*, *H. aspersa*, *H. rufescens*, *H. hispida*, *H. nemoralis*, *H. hortensis*, *Hyalinia cellaria*, etc.

Mr. C. E. Wright detected a run of these creatures, about ten yards long, beneath the thick grass and nettles in a quarry near Lincoln, along the whole length of which broken shells were so thickly strewn that in the space of twelve inches he counted distinct remains of ninety-six shells of *Helix nemoralis* and *H. hortensis*, besides those of a number of smaller species, which would give a total of about three thousand shells in this restricted area. So eager and acute are mice in the pursuit of their prey that during winter they have been known to burrow into the thick snow to gain access to the hybernating *Helices* of whose presence beneath they were apparently aware; while the Water Shrew dives beneath the surface to secure *Limnæa auricularia* and *Planorbis corneus* for food.

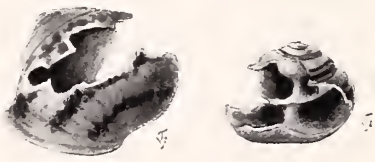


Fig. 729. Fig. 730.

Fig. 729, *Helix aspersa* Müll., and Fig. 730, *Helix nemoralis* L., illustrating the manner in which they are destroyed by Field-Mice.
Collected by Mr. C. E. Wright in an ironstone quarry at Lincoln.

Otters and rats have also been recorded as preying upon freshwater mollusks, breaking away the ventral margin of the valves of the *Anodontæ*, etc., with their teeth to gain ready access to the animal inhabitant.

The Hedgehog has been deemed by many observers to be one of the most persistent enemies of land shells, while the Fox is accused of regaling himself in winter upon them when more substantial food is difficult to obtain. Rabbits are also accused of occasionally devouring *Helix aspersa* and other of the larger species, and justly so, judging by the number of gnawed empty shells strewn about their burrows and the absence of traces of any other animal likely to cause the destruction amongst them.

Birds are especially destructive to molluscan life, the insectivorous species making mollusks a staple article of their diet during the winter months. The Thrush tribe at all times, but especially in winter, feed

largely upon *Helix nemoralis*, *H. hortensis*, and other species, seizing the shell by the outer lip, and striking it repeatedly against a stone until broken, or fixing the shell in some suitable crevice and pecking at it until fractured, a particular stone being often selected to which the shells are carried for the purpose of being broken thereon. These sacrificial stones, known as "Thrushes' altars," are usually in open positions and easily recognized, not only by their slimy surface and the shell-fragments adherent thereto, but by the little heaps of broken shells which are strewn around them.

Fig. 731.

Fig. 732.

Figs. 731 and 732, *Helix nemoralis* L., illustrating the manner in which these shells are broken by Thrushes, etc. Collected by Mr. C. E. Wright, near Kettering.

Starlings, Fieldfares, Redwings, and many other birds devour great quantities of the smaller species during the winter months, *Zua lubrica* being a favourite food of the Starling, while the Fieldfare and Redwing search for *Helix virgata* and other species. In times of stress the Goldcrest resorts to the same food, seeking out from their hiding-places *Balea*, *Clausilia bidentata*, *Pupa muscorum*, etc. The Bearded Titmouse and Reed Bunting devour great quantities of the *Succineæ*; the Titlark searches for *Helix caperata* to vary or make up for the deficiencies of its more favourite coleopterous diet, and the Grey Wagtail preys upon *Ancylus fluviatilis* and *Sphærium corneum* in our streams and ponds.

The Heron feeds upon *Limnæa stagnalis* and other species and also upon the *Anodons*, with which it will fly up into the trees, breaking the shell against the branches; the Hooded and Carrion Crows, which also feed upon the same species, have been observed to carry them to a considerable height and to drop them to the ground to break the shell, so that they can more readily get at the animal.

The Dipper haunts the rocky streams, and the Water-Rail the pools, preying upon the mollusks and other aquatic creatures therein, while the Land-Rail is said to become quite fat in the summer months by feeding upon the various snails.

The Batrachians are also very partial to mollusks, Frogs and Toads more especially devouring considerable quantities on occasions, and this is so well known that the garden attached to the laboratory of Agricultural Chemistry at Rouen by the introduction thereto of 100 toads and 90 frogs was in a month completely cleared of the slugs and snails which had previously so infested it that the growth of any useful

plant had been quite impossible. The Frogs and Newts also eat the different species of *Limnæa* and *Planorbis* of our ponds and streams.

Fish in general are very partial to the mollusca, feeding greedily upon them, and the havoc thus caused amongst the marine species by the enormous numbers they consume has been frequently chronicled, but the destruction amongst the freshwater species has not attracted so much attention.

The beneficial effect of water-snails as nourishing food, especially for trout, is shown by the rapid growth of fish placed in streams or ponds in which mollusks abound. The ravages of fish amongst mollusks are not, however, confined to such species as disport themselves more or less actively at the surface or amongst the vegetation, but is also carried on amongst the minute mud-loving *Pisidia*, which in America have been shown to be an important food of the Whitefish.

The Gillaroo Trout, which lives in the Irish loughs, and other famous breeds also, subsist chiefly upon mollusks which give them the exquisite flavour which has rendered them so famous and prized by epicures. Specimens of the Gillaroo Trout have been caught gorged to repletion with *Bithynia tentaculata* and other freshwater species, and the remarkable and peculiar thickening of the stomach-walls of this trout has been attributed to the fact of shelled snails forming so large a part of its diet.

The Eel is another rapacious devourer of the mollusca, as many as 350 shells of *Valvata piscinalis*, in addition to those of other species, having been obtained from the stomach of a single eel.

The Barbel has been noted as having a special predilection for *Valvata piscinalis* and also for *Sphærium corneum*, and many fish, and more especially gold carp, regard *Physa fontinalis* as a choice and delicate morsel, while the Roach is recorded to feed even upon the eggs of the various species.

The Coleoptera prey freely upon the mollusca, the *Dytiscus marginalis* being particularly destructive to the Limnæidæ generally, but apparently preferring *Limnæa stagnalis* to other species, although accumulations of the shells of *Planorbis corneus* with the sides of the whorls bitten away, to allow of easy access to the animal, have been recorded as the work of this species.

The *Silphidæ* also destroy the smaller land species, the Rev. A. H. Cooke stating that they fracture the shells by striking them against their own prothorax.

Drilus, a coleopteron allied to the glow-worm, and also its larva, attacks and devours *Helix nemoralis*, *H. hortensis*, and *H. aspersa*, the larva taking up its abode within the shell of its victim, exchanging its domicile when necessary by attacking a larger individual, and appropriating the shell, enclosing itself within it by a fibrous web before undergoing its metamorphoses. The beetle emerges as an imago in October, when the molluscs again begin to be torpid.

The species of the genera *Cychrus*, *Carabus*, and the families *Staphylinidæ* and *Hydrophilidæ* all prey more or less eagerly upon snails, the attenuate head and prothorax of the *Cychri* enabling them to readily insinuate themselves within the shell of their victims; the larvæ of all these groups are also very voracious, while the larva of the Glow-worm, which feeds almost exclusively on small mollusks, is believed by Fowler to derive its phosphorescent powers from this source.

Ants have been observed by Mr. E. J. Lowe to ferociously attack and destroy snails as large as *Helix aspersa* when they have ventured too near the nests. In one case more than a hundred empty shells of that species found near a large ant's nest were considered to be remains of mollusks destroyed by the ants.

Although the enemies of the mollusca are almost legion, and include members from almost every class of the animal kingdom and so destructive that it is marvellous that any individuals escape their numerous foes and live to perpetuate the race, yet, in addition to them, there are also enemies even amongst their own ranks which are scarcely less destructive than their more legitimate foes.

In the British Isles although many species intermittently display malacovorous or cannibalistic propensities, such habits are not normal, but often induced by hunger, or other excitant, *Hyalinia lucida* being perhaps the most readily addicted to gratifying its cannibalistic tastes.

Many foreign genera are, however, strictly and exclusively malacovorous, feeding chiefly upon the phytophagous species of snails. In South Africa the great *Aerope caffra* eagerly pursues and greedily devours the *Helix aspersa* which has accidentally or purposely been introduced into that country, while in North America, at Charlestown, South Carolina, the introduced *Rumina decollata* is said to be exterminating the *Helix nemoralis*, which was also a flourishing colony in that city.

In addition to the destruction due to active effort, the *Unionidæ* are sometimes killed mechanically by the agglomeration of *Dreissensia polymorpha* upon their valves, preventing them opening for respiratory and other purposes.

Parasites are organisms which at any period of their lives are dependent for food, shelter, or protection, upon some other animal or animals, with whose welfare they are, therefore, vitally concerned, and consequently they do not at any time destroy their host, although some forms are known to be the cause of castration in *Helix aspersa* and other species.

They are not, as formerly believed, present within or upon the body only as a result of the diseased or vitiated condition of the blood or tissues of the host, and therefore necessarily indicative of an unhealthy condition of the body, nor is there a special class or race of parasites, corresponding to that of birds, reptiles, or other groups, as all the classes of the animal kingdom have given off from their inferior ranks some branches in this direction, probably consisting of those weaker forms which being unable to successfully compete with the newer and stronger races which have successively been evolved have, in order to avoid extermination, been compelled to adopt a parasitic life, their form becoming modified and degenerating by the atrophy of the organs unsuited to their adopted life. From the severity of the life competition, parasites have become so numerous that there are few or probably no animals which do not entertain a more or less numerous party.

The parasitic organisms dependent upon the mollusca are, with a few exceptions, little known, and the cycles of life which many undergo have only been thoroughly worked out in one or two species, but it is certain that many of our native species harbour one or more of these creatures and thus provide them with food and shelter, while several of our mollusks are known to be liable to be infested by eight or ten quite distinct species, which either affix themselves upon the exterior of the body or live amongst the viscera, and may even be found in the pericardial cavity. One species at least, though not in this country, is infested by a species of fish which makes use of mollusks as a nidus for its ova, the embryos being hatched and developed amongst the branchial filaments. The young mollusks of the same family are, however, themselves parasitic upon fishes, affixing themselves to and deriving nourishment from their hosts.

True parasites are entirely dependent upon, and unable to exist apart from, their hosts, as their alimentary canal has become degenerate and their nourishment is derived solely from the fluids of their host, which are constantly being absorbed through the general integument and assimilated by the animal independent of its will. Mutualists, commensals, or messmates, however, only avail themselves of the shelter and protection that close proximity affords, feeding independently of or in company with their entertainer.

Parasites, according to their habits and modes of life, may, for our purpose, be divided into three sections, Ecto-parasites, Endo-parasites, and Commensals.

The ENDO-PARASITES of the mollusca are chiefly drawn from the Trematodes, a large number of whose species pass through one or more of the intermediate stages of their life's cycle within the bodies of various mollusks, many attaining their perfect or sexual development within the body of some vertebrate; each species is, however, more

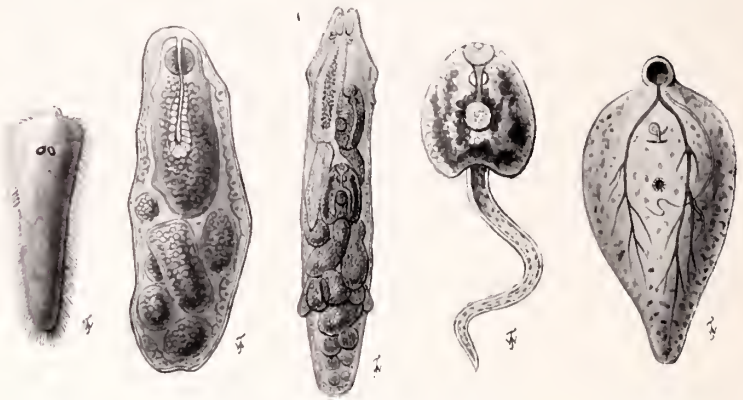


FIG. 733. FIG. 734. FIG. 735. FIG. 736. FIG. 737.

Fasciola hepatica, an endodermic parasite, showing the successive stages through which this species passes before attaining sexual maturity (highly magnified, after Marshall and Van Beneden).

FIG. 733.—Free ciliated embryo.

FIG. 734.—Sporocyst, as living usually in lung cavity of *Limnæa truncatula*.

FIG. 735.—Redia, as living amongst the viscera and especially within the digestive gland of the mollusk into which it has migrated from the lung cavity.

FIG. 736.—Cercarian stage which has escaped from the mollusk and again become free, eventually encysting upon the grass and being eaten by sheep.

FIG. 737.—The mature sexual *Distoma*, as developed from the cercarian stage within the bile ducts of sheep.

or less restricted not only to particular species, but to special or determinate parts or organs thereof.

These flat or soft worms usually begin existence by following a free aquatic life, travelling by the aid of a ciliated investment and eventually effecting a lodgment within the body of the first suitable animal

they encounter, which is usually a mollusk, becoming scolices or vesicular worms amongst the connective tissue, muscles, etc., but at a later stage occupying the digestive or respiratory passages which are in free communication with the exterior.

The Ecto-Parasites are not nearly so numerous, the best known examples being the *Acari*, found so commonly upon the bodies of the terrestrial species, and the species of *Atax*, which infest the *Unionidæ*.

The *Conchophthirus* lives within and probably subsists upon the body mucilage of various mollusks, both univalve and bivalve, while *Chætogaster*, *Matzia*, and other forms live within the respiratory or mantle cavity of different species.

Amongst the Ecto-Parasites must also be placed the *Micrococcus conchivorus*, a protophyte upon the shells and destroying its outer layers, a process in which the species of *Batrachospermum*, *Chætophora*, and other cryptogams assist.

Fig. 738.—An Ectodermic Parasite from *Hyalinia cellaria* (Müll.), *Philodromus limacum* Jenyns × 30.

Fig. 739.—A Commensal, Messmate, or Mutualist, *Epistylis coarctata* Clap. and Lach., a colony stock (highly magnified after Saville Kent).

The Commensals or Mutualists are also often derived from the lower ranks of the animal world, and simply make use of the shell or body of the mollusk as an abode or place of fixation, and in such positions we may frequently find forests of *Vorticella* and other Infusoria. That these colonies are not always harmless has been demonstrated by Mr. R. Standen, who has established the probability that suitably-placed colonies of *Epistylis* or other urticating genera are often responsible for the scalarid and other monstrosities of *Planorbis spirorbis* and doubtless other species.

The Uses of the land and fresh-water mollusca in this country for food, ornament, medicine, or in the Arts are neither numerous nor important. Probably, however, the principal value of the mollusca to the human race generally is that they provide us directly and indirectly with abundance of food, and although the terrestrial mollusca

are not generally used in this country as aliment, yet in some districts they are freely consumed either for nourishment or medicinally; in other and warmer countries, however, their use as food is much more general and comparatively small species are utilized for this purpose.

As Food, the snail was one of the creeping things denounced in Scripture (Leviticus, cap. xi.) as unclean, and its use for that purpose forbidden, yet the larger kinds of testaceous land snails have been held in repute in all ages, even by the Chinese and Hebrews for their alimentary or curative properties, and the masses of *Helix* shells found in the caverns inhabited by the primitive men of the Stone Age, probably indicate the indulgence of similar tastes by these savage races, while kjokkenmöddings or heaps of kitchen refuse, formed by countless generations of extinct pre-historic peoples, are found in the United States, Brazil, Australia, New Zealand, Denmark, Scotland, Ireland, England, etc. These immense mounds are sometimes hundreds of yards in length, and largely composed of the shells of edible mollusks, bones of mammals, birds and fish, broken pottery and primitive implements of bone or other material, and occasionally contain terrestrial mollusca, as in Denmark, in which *Helix nemoralis* is found, while *Helix aspersa* has been recorded from a neolithic kitchen-midden at Hastings, and from deposits resembling kitchen-middens about a mile from the present banks of the Mersey, while those of Florida have been noted to contain freshwater species.

The predilection of the Romans for this food is widely known, although this is stated to have been due, not to any special relish for such an insipid article of diet, but to a belief in its aphrodisiacal virtues. The prevalence of Helicophagy among the Romans was, however, so universal that they not only collected snails and imported the more delicate and esteemed kinds from Illyria, Africa and other places, but bred and fattened them for the table in specially arranged farms or Cochlearia, a plan originated by Fulvinus Hirpinus, at Tarquinium, about 50 B.C. These Cochlearia were preferably somewhat shaded areas, encompassed by water, where in addition to the growing vegetation, the snails were fed upon sodden wine dregs, bran, flour and various aromatic herbs, and under this generous diet they acquired a refined flavour and grew to a good size. This taste is also evidenced by the use amongst them of an utensil, made from bone, silver or other material, termed a Cochleare, especially adapted for this purpose. This little implement had one end fashioned like an

ordinary egg-spoon, while the other end was pointed for the purpose of hooking the snail from its shell. That its name Cochleare was derived from its usage may be inferred from the epigram by Martial:

"Sum cochleis habilis, sed nec minus utilis ovis,
Namquid scis potius cur Cochleare vocer,"

which Sir W. W. Gull has freely rendered as

"I am clever at Winkles, for eggs not less fit,
Then why I'm called Cochleare question your wit."

Fig. 740.—Cochleare, or Roman silver spoon, found at Little Horwood, Buckinghamshire, reduced to about half size of original (from Sir John Evans' collection).

Fig. 741.—Cochleare, or Roman silver spoon, found near Woodchester, Gloucestershire, reduced to about half size of original (from Sir John Evans' collection).

Fig. 742.—Cochleare, or Roman silver spoon, found in the Thames, reduced to about half size of original (from Sir John Evans' collection).

In mediæval times snails were especially reserved in Denmark as a privileged article of food for the nobility and gentry.

At the present day snails are largely used for human food in the warmer countries of Europe and elsewhere, more especially during the Lenten season, as the Roman Church permit their use as food during that period. They are stated to contain 17 % of nitrogenous matter and to equal the oyster in nutritive properties.

Snails are to this day cultivated for food in various parts of Europe in special Snail-farms or Escargotières. One at Chalet St. Denis, near Fribourg, described by Mr. R. D. Darbishire, which fattens sixty to eighty thousand *Helix pomatia* annually, consists of a large meadow fenced in by boards about a foot high. The snails annually needed to restock the farm are gathered every spring in the vicinity of the farm by the farm labourers and at once placed on one-half the meadow and left there until July, when they are transferred to the other half of the field, which is divided by hoardings, about a foot high, into numerous square spaces which are filled with moss, the snails being fed therein upon cabbage until they become very fat and of a greenish-

white colour. Towards September the snails burrow into and hide amongst the moss with the aperture upward and closed by the calcareous winter epiphragm. In this condition they can be exported and are worth 17 francs per 1,000; some, however, do not form epiphragms and, as they must be used more quickly, only realise 10 francs per 1,000. Paris alone is said to consume fifty tons daily when in season, the most esteemed kinds coming chiefly from Dauphiné and Burgundy.

Snail eating is also very prevalent in Spain, where snails are recognized articles of commerce, the women who deal in them, known as Caracoles (from *Caracole*, a snail) congregate in the Snail market with their baskets of snails before them, crying their wares and occasionally cracking a shell with their teeth to convince buyers of the quality.

In more remote countries many species belonging to genera not generally considered edible in Europe, are consumed as articles of food, *Neritina* by the inhabitants of Mauritius and Guadeloupe, and *Uniones* and *Neritinæ* by the natives of the Solomon Isles, *Vivipara* by those of Cambodia, *Bulimi* by the New Caledonians, while *Anodonta edulis* is regularly reared for food by the Chinese in the ditches of Song-Kiang-Fou.

In this country, although several species of marine mollusca are universally used and more or less highly valued as dainty or appetising food, the non-marine species are not nearly so generally utilized for the purpose, probably on account of the greater insipidity of their flesh. In some parts of the British Isles, more especially in the western districts, *Helix aspersa* is, however, held in good repute as an excellent article of diet. The glass-blowers and others about Bristol, Knottingley, in Yorkshire, and other places, not only use *Helix aspersa* for food but consider it a cure for consumption, and so great is the demand that in Bristol it furnishes a somewhat regular occupation to gather them, as in summer, when considered unfit for human food, they are used as food for ducks. Dr. Gray records that the glass-workers of Newcastle formerly held an annual snail-feast, collecting the snails themselves the Sunday before the feast, and the working-men of Lancashire had the reputation of indulging in a similar custom.

The *Unionidæ* generally are considered edible in some districts and are eagerly consumed in the poorer districts of Southern Europe,

when roasted and dipped in oil or scattered over with bread crumbs and scalloped. *Unio margaritifer* was formerly considered as one of the daintiest of foods, and the *Anodontæ* are considered edible in many places abroad and are also eaten by the peasantry around Lough Schur, Leitrim.

As MEDICINE, the Ancients considered the slugs and certain snails to possess extraordinary virtues and attributed sovereign powers to them in the treatment of various disorders. According to the then current belief there was scarcely an ailment to which men or domestic animals were liable which could not be cured by the proper use of preparations of these animals. This exaggerated estimate of the efficacy of these objects has been transmitted through many centuries, and in some secluded and unsophisticated districts the belief in the manifold virtues of these or similar remedies still exist.

The testaceous species, however, never appear to have attained the celebrity in medicine acquired by the naked mollusks, but were more used as articles of food, although in common with them, they have had, even in comparatively modern times, a widely extended use, and were considered a cure for Ague, Scrofula, Dropsy, Pleurisy, Fevers, Asthma, Consumption and Pulmonary complaints generally, either consumed living or prepared in a variety of ways, which were thought to best conserve their efficacy.

Arion ater, Limax maximus, L. flavus, Helix aspersa, H. nemoralis, H. hortensis and *H. arbustorum* all at one time occupied places in the Materia Medica or were the base of pharmaceutical preparations, and even pearls long maintained a great medicinal reputation, a celebrity due to the testimony of the Arabian physicians.

The Limacelle or internal shell of the Slug was held in high repute as an exceptionally powerful remedial agent for toothache, the pains being said to instantly cease when the little calcareous grains formed in *Arion* are placed in the hollow tooth.

For dysentery, it was recommended that five slugs (preferably African ones) be burned and mixed with the weight of a demi-denier of Acacia, and two-spoonsful of this mixture to be taken in Myrtle or other thick wine, with an equal quantity of warm-water, or in severe cases to be administered as a clyster.

For healing ulcers, the ashes of Dormice, Wild Rats, Earthworms and Slugs mixed with oil was considered very efficacious. The ashes of burnt slugs were also believed to be especially powerful in healing

all ulcers of the foot, and Marcellus Empiricus recommended the same as a remedy for hydrocephalus in children, while Kiranides prescribed the application of a slug pounded, with incense, to arrest bleeding at the nose.

Snails prepared in various ways used to be highly esteemed as a cure for various injuries and diseases, ancient physicians regarding snails pounded up with their shells as a remedy endowed with discutient and resolvent properties, and the shell alone, when powdered, as a diuretic.

Pliny, the elder, recommended snails for a cough or for pains in the stomach, but it was considered essential that an uneven number should be taken.

It is, however, in the treatment of pulmonary complaints that the greatest celebrity has been attained and in consumption the use of preparations of *Helix aspersa* and *Helix pomatia* are said on good evidence to be strikingly effectual. Lovell Reeve, in his "British Land and Freshwater Shells," published in 1862, says: "Mr. Barlow, of the firm of John Dickinson and Co., paper-makers, informs me that he has a brother who was in the last stage of consumption, when their father resolved to try the experiment of a diet of Apple Snails. The expressed mucilaginous juice of the snail was administered to the patient, without his knowledge, in every conceivable form. It was taken in jellies and conserves, in gravies and with entremêts of meats. In the course of a twelvemonth the invalid was entirely cured and went to the Crimea, and is living at this moment a strong hearty man."

Slugs have comparatively recently been recommended in cases of consumption by medical men. A relative of my own, who in his youth was considered to have consumptive tendencies, by advice made *Agriolimax agrestis* a regular article of diet for some time, and in his later years certainly showed no evidence of consumptive taint.

In this country when medicinally used for pulmonary complaints or consumption they may be boiled in milk or made into a mucilaginous broth, but may also be eaten alive or, if a shelled species, the shell pricked through with a large pin to enable the patient to suck the oozing liquor.

Snail syrup, prepared by passing a stout thread through the shell and body of a number of snails, and suspending them over a dish of coarse brown sugar, upon which their mucilaginous exudations are

allowed to drop, is recommended by the village dames of Sussex as a specific for coughs and colds.

Figuier has extracted from Helices an odorous and sulphurous animal oil, which he has named Helicine, by means of which Dr. Lemare is stated to have radically cured cases of consumption.

In Martin Lister's time snails, and particularly *Helix pomatia*, had long been considered as restorative in hectic fever cases.

In modern times preparations from snails have been employed by qualified medical men for the treatment of many disorders, Mr. W. G. Binney recording that in 1863 the Syrup of Snails was prescribed to ailing members of his family by two regular French physicians in Paris.

A liniment of great local repute, for the relief or cure of Lumbago, Rheumatism, Bruises, Sprains, etc., etc., was formerly prepared by the late Mr. John Crowther, of Pontefract, by placing a number of *Helix aspersa* within a large tin vessel, upon a warm boiler, the dark-brown oily matter derived from their desiccation when mixed with ammonia being ready for use.

In Veterinary medicine, Puton records that the husbandmen of the Vosges used the calcined and powdered shells of Helices to destroy the films that form on the eyes of domestic animals.

The Minor Uses of the mollusca are very various and often very localized, the shells of mollusks are said to have been used as

Drinking Vessels by the Ancient Britons, and to have been the only ones generally possessed by them; the Highlanders, in the more secluded districts, are said even yet to use them for the same purpose.

As Cream Skimmers, the thin-edged valves of *Anodon* and *Unio* have frequently been used in many country districts, and those of *Unio margaritifer* are, or were recently, used in the Isle of Man as scoops and as porridge spoons; while the shells of *Helix pomatia* are used in France among Peach and Apple trees as traps for earwigs, etc.

As Colour receptacles, the valves of *Unio pictorum* were formerly employed by Flemish painters and, though they are now quite obsolete for this purpose, they may still be occasionally obtained containing a preparation of gold and silver for illuminating, though even for this purpose the shells of *Mytilus edulis* seem now more in vogue.

For Button-making and other purposes, the nacreous or mother-o'-pearl lining of the Uniones has been used commercially, and when finely pulverized it makes a very excellent polishing powder for hard

materials, while the aborigines of Port Curtis, Queensland, polish their spears, boomerangs and waddies with the sharp edges of broken shells of *Helix cunninghami*.

Colour of a somewhat brilliant violet, used by the mural painters of the sixteenth century, is stated by Dumas and Persoz to have been yielded by finely pulverized shells of *Neritina fluviatilis*.

As Manure, *Dreissensia polymorpha*, which often exists in such incredible numbers within a very limited area, has been used with excellent effect in Lancashire for enriching the land.

Fertilization of Flowers may probably be sometimes accomplished by mollusks crawling over them during cold or damp weather when insects are not abroad. Magnus has recorded and especially noticed the actuality of this process with *Agriolimax lævis* and *Chrysanthemum vulgare*.

Cement was made in Lister's time by pricking the body of *Helix aspersa* and collecting the fluid exuding therefrom, which when mixed with an equal quantity of albumen and quicklime and well pounded, form a durable and excellent cement for marble or stone, hardening almost immediately.

Pounded snails were used at Montpellier to moisten the wooden moulds, to prevent the adherence thereto of the wax figures and allowing them to come easily away with a fine surface, and are said also to have been formerly successfully utilized in the manufacture or adulteration of cream.

As Food for Sheep, *Helix virgata* especially has long been credited with contributing materially to the nourishment of sheep and as being responsible for the superior flavour of the South Down and Dartmoor mutton, as it is quite impossible for the sheep to pasture on the downs without devouring immense numbers of these snails.

This excessive abundance of *Helix virgata*, in some favoured localities, is so remarkable as to have originated the sensational reports of "showers of snails," when these animals have appeared suddenly from their hiding places in vast numbers after rain, following upon a period of dry weather.

As Food for Fishes, the mollusks are very important and it is a very prevalent belief that in rivers where *Unio margaritifer* exists the trout fishing is markedly improved; while in America the smaller *Pisidia* have been shown to form one of the most important articles of food of the Whitefish. According to Mr. Sturges Dodd, the

Barbel, Roach, Rudd, Chub, Grayling, Gudgeon, Bream, Perch, and Burbot all feed upon aquatic mollusks.

As Bait, *Anodon*, *Unio* and *Vivipara* are much used by fishermen, *Unio margaritifer* especially being so employed, many boat loads being said to be taken from the mouth of the Ythen, near Aberdeen, and employed in the Cod and Ling fishery; the use of *Dreissensia*, as bait for Perch, by an angler led to the discovery of its existence in this country; while the larger *Limnææ* are successfully used for bait by the Leicestershire anglers.

As Money, certain shells, either in their natural state or worked into particular shapes and strung together, forming Wampum, have been almost universally used as money or as a medium for barter by all savage and barbarous races, and although marine species are almost invariably used for the purpose, yet Wampum was formerly made from the shells of the *Unionidæ* by the Indians of New Brunswick, Canada, and *Achatina monetaria* is similarly used by the natives of Benguela.

For Decorative purposes or for personal ornamentation the Pearl is "par excellence" the most prized object furnished by the mollusca, yet the shells themselves, wholly or in part of many marine species,

Fig. 743.—Helicidian necklace, made by the peasantry of Donegal, and composed solely of *Helix nemoralis*, reduced to one-fourth natural size (Mr. R. Welch's collection).

are much used by savage tribes for the same purpose, their brilliancy and attractiveness being so superior to that of the non-marine forms, which are, however, occasionally used for personal decoration, as in South America, where the aborigines use the shells of *Ampullaria*, *Orthalicus*, *Labyrinthus* and *Bulimulus* for ornamenting the elaborate

cloaks worn by women of rank, while the large *Bulimi* are worn as breast ornaments and for other purposes. In the Island of Iona, *Helix itala* and *Helix acuta* are strung together to form necklaces, and at Bundoran, in Donegal, and elsewhere, *Helix nemoralis* is similarly employed, a practice regarded by Mr. Welch as a survival of a prehistoric custom. The primitive men of the stone age probably also adorned themselves with similar ornaments, as is testified by the pierced shells of various species found in the caverns they frequented in South-Western France, among which numerous shells of *Vivipara lenta* are found, probably procured from the Isle of Wight, where they are now so abundant in a fossil state.

From the earliest times preparations have been made from snails, which were believed to be beneficial to the complexion, and comparatively recently the liquid procured from them by distillation was used by ladies to give whiteness and freshness to the complexion.

Superstitious reverence, in one form or another, has been accorded to the mollusca by the more ignorant and credulous people of every age, due to the emblematic exaltation of certain forms as symbolic of the vital phase of religious faith, or to the imaginery popular belief in their efficacy as charms or amulets to ward off or protect the wearer from injury or disease.

In ancient times the Egyptians venerated the Scarabæus or Sacred Beetle as typifying in its life-history the resurrection, and in like manner the Gauls and Ancient Britons reverenced the Snail, as a visible emblem or symbol of our resurrection and immortality, the image of a shell so often found sculptured within the ancient Gallic tombs, being emblematically expressive of the belief of these primitive people in man's resurrection and immortal life, and possibly the presence of Helix shells in ancient British burrows and tumuli may have some similar significance.

The Romans habitually ate snails at their funeral repasts around the tombs of those dear to them or at those of persons whose memory they wished to honour, the evidence of the prevalence of this custom is found in the masses of shells strewn about the cemeteries of Pompeii. This incorporation of the snail among their funeral ceremonies being probably a relic of the still older belief in the existence of some mysterious link between the grave, silent snail and the spirit of their ancestors, a superstition probably originating from the circumstance of finding snails living within the vaults of their forefathers,

and the gradual attribution to them of a sympathetic attraction and affection for the places of sepulchre where repose the dead.

The Romans, who derived many of their superstitions from the Greeks, especially reverenced the internal shells of the slugs, believing them to be powerfully curative in cases of tertian, quartan and intermittent fevers when worn around the neck of the patient and falling towards the heart, and that diseases of the head or headaches were cured by carrying the shell upon the person or rubbing the forehead with the minced or pounded animal; while the granular substance representing the shell in *Arion*, if suspended from the necks of infants, was firmly believed to facilitate teething.

Warts are believed by many rural folk to be easily removable if a living slug be rubbed over the affected part and the animal then impaled upon a thorn, in some secluded place, and left to die. As the snail dies and gradually shrivels up, the wart, being impregnated with its matter, will shortly do the same and gradually disappear.

Worn fragments of shells or Snail-stones were formerly esteemed in the Scottish Highlands and in Guernsey as a remedy for affections of the eyes, but the Snail-stone of Scotland, to which many mysterious virtues were long ascribed, was merely a piece of blue glass.

In some barbarous countries many species, especially if sinistrally coiled, are reverenced as sacred, or as charms protecting the owner from evil spirits or disease.

The Kabyles of Algeria perforate the ends of the valves of *Unio pictorum*, which they call thimah'rin, and suspend them around the necks of their children as Amulets, believing them to be a powerful protection against evil influences.

The negroes of Prince's Islands formerly were in the habit of suspending a string of *Helix bicarinata* above the doors of their cabins, as an act pleasing to the gods and calculated to secure their protection; while *Achatina perdix* was formerly forbidden to be exported from the East Indies, probably from some ancient superstition regarding it.

Reversed varieties of the *Turbonilla* or Chank Shell are held sacred in the far East. In India the God Vishnu is represented holding this shell in his hand, while in China they are kept in the Temples, and used only for anointing the Emperor on his coronation, for the administration of medicine on important occasions, and for bestowal by the Emperor upon high officials, whose duties oblige them to cross

the sea, as the sacred shell when blown is believed to have power to still the waves and thus ensure safe voyages.

Snails have, however, at times fallen under the ban of the Church, and a prayer of the holy martyr, Trypho of Lampsacus, who lived about the tenth century A.D., contains the following quaint exorcism directed against them.

> "O ye Caterpillers, Worms, Beetles, Locusts, Grasshoppers, Woolly-Bears, Wireworms, Longlegs, Ants, Lice, Bugs, Skippers, Cankerworms, Palmerworms, Snails, Earwigs, and all other creatures that cling to and wither the fruit of the Grape and all other herbs, I charge you by the many-eyed Cherubim and by the six-winged Seraphim, which fly around the Throne, and the holy Angels, and all the Powers, etc., etc., hurt not the Vines nor the land nor the fruit of the trees nor the vegetables of ———, the servant of the Lord, but depart into the wild mountains, into the unfruitful woods, in which God hath given you your daily food."

Augury or Soothsaying, to foretell the result of any impending conflict, is practised in Japan and other places by means of *Vivipara japonica*, specimens of which are placed at opposite corners of a tray to represent the belligerents and those advancing reveal the conquering party.

The Sea Dyaks of Sarawak similarly establish the guilt or innocence of accused persons, by the accuser and accused each selecting a land shell, upon which lemon juice is squeezed, the one moving first shows the guilt or innocence of its owner, according as rest or motion has been agreed upon to prove the case.

Divination, even at this day, is said to be practised by the rustic English and Irish maidens who believe that, if on May-day morning, the small white slug (*Agriolimax agrestis*?) be placed upon the hearth or other smooth surface lightly sprinkled with flour or fine dust, it will by its track describe thereon and thus reveal the initial of their unknown lover's name.

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A

MONOGRAPH

OF THE

LAND & FRESHWATER MOLLUSCA

OF THE

BRITISH ISLES.

BY

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PART II. (Issued Aug. 24th, 1895).

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OF THE

LAND & FRESHWATER MOLLUSCA

OF THE

BRITISH ISLES.

BY

JOHN W. TAYLOR, F.L.S.,

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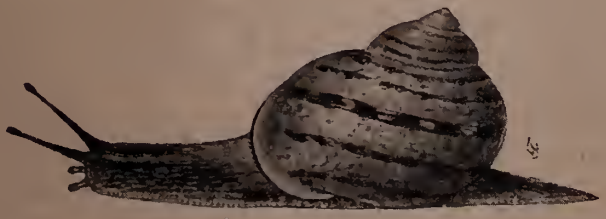

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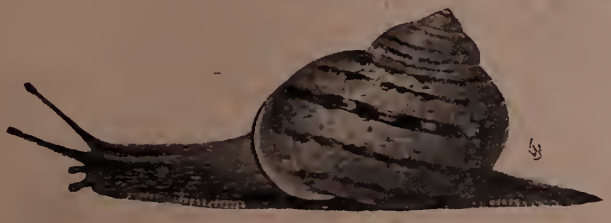

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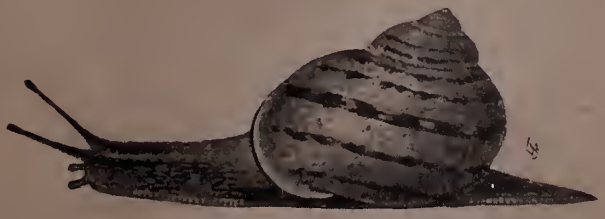

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A

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LAND & FRESHWATER MOLLUSCA

OF THE

BRITISH ISLES.

BY

JOHN W. TAYLOR, F.L.S.,

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EX-PRESIDENT OF THE CONCHOLOGICAL SOCIETY OF GREAT BRITAIN AND IRELAND,
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